ACOUSTIC COMMUNICATION OF RED SQUIRRELS (*TAMIASCIURUS HUDSONICUS*): FIELD OBSERVATIONS AND PLAYBACK EXPERIMENTS

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Stephen George Frost

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The spectrum of sciurid social systems ranges from the highly social prairie dogs (Cynomys) on one end to the solitary red squirrels (Tamiasciurus) on the other. Vocalizations play an important part in the social communication throughout the spectrum but the red squirrels (T. hudsonicus and T. douglasii; Rodentia, Sciuridae) are considered the most vocal of the squirrels by many and it is unusual to observe them in the field without hearing one or more vocalizations.

The Douglas squirrel is restricted to the Pacific northwest (including parts of British Columbia, Washington, Oregon, and California) while the range of the red squirrel extends from the eastern deciduous forests through the northern boreal forests of Canada north to Alaska and as far south as New Mexico in the Rocky Mountains.

The red squirrel and Douglas' squirrel are so closely related that their appearance and behavior are similar and they are known to produce hybrids in nature (Smith, 1965; 1968). The existence of very little overlap in the two squirrels' distributions can be in part attributed to competition, but Smith (1970) indicates that each species is adapted to a slightly different food niche. Seeds from conifer cones form a large part of the squirrels' diets, but when the broad variety of T. hudsonicus's habitats takes it away from conifers and into the eastern hardwood forests, its fare becomes similar to that of the gray and fox squirrels (Sciurus carolinensis and S. niger respectively). The diversity of food consumed by

T. hudsonicus can be seen in the lists made by Klugh (1927), Hatt (1929), and Layne (1954). T. douglasii is necessarily more restricted in its diet due to its limited range and habitat. The squirrels of this genus are considered solitary and highly territorial during the non-breeding season, although red squirrels will share a nest during the winter and sometimes tolerate conspecifics very close to them when feeding on seeds or cones that are localized and/or highly abundant. These squirrels may have two litters per year but there is generally only one litter in the more northerly reaches of the range. Three to seven young are born after a 36 to 40 day gestation.

The red squirrel has been shown to have a bimodal daily activity pattern peaking just after sunrise and just before sunset (Hamilton, 1939; Layne, 1954). Cold winter weather can change this so that the squirrel is only active during the warmest mid-day period.

Although many early papers on red squirrel biology described vocalizations in a subjective fashion (Gordon, 1936; Hamilton, 1939; Hatt, 1929; Klugh, 1927; Layne, 1954; and Svihla, 1930), not until quantitative spectral analysis of the vocalizations were accomplished could the vocalizations described by different authors be adequately compared. Using sound spectrograms, Smith (1965, 1968) described five call types for the two species of Tamiasciurus and their proposed functions. Embry (1970), also using spectral analysis, described six types of vocalizations for T. hudsonicus and attributes possible functions to them. Such studies have indicated,

however, some variation in attributed function as well as in spectral qualities for particular call types.

Observational techniques have been widely used in arriving at the functions of vocalizations in tree squirrels (e.g. Embry, 1970, T. hudsonicus; Farentinos, 1974, S. aberti; Horwich, 1972, S. carolinensis; Smith, 1965, 1968, T. hudsonicus and T. douglasii; and Zelley, 1971, S. niger). Dunford's (1970) use of playback experiments (directing pre-recorded vocalizations at one or more subjects) in his work on the spatial organization of the chipmunk, Tamias striatus, indicated that the "chipping" vocalization partially inhibits other chipmunks from approaching the vocalizing animal. Searing (1975) used playback experiments on red squirrels in interior Alaska to test the response of squirrels to vocalizations he considered aggressive calls and his results will be discussed in this paper. I know of no other studies using playbacks on Sciurids nor any that have information on sound levels of squirrel vocalizations.

The purpose of this research was to 1) record and describe the different vocalizations used by the red squirrel, 2) to collect quantitative information on sound levels of red squirrel vocalizations, 3) develop suitable techniques for field playback experiments, 4) record behavioral responses of red squirrels to playbacks of particular vocalizations, and 5) determine the function of the various vocalizations via playback experiments and observation of behavior.

MATERIALS AND METHODS

Study Site

The field work of this study was conducted from December 1974 through May 1976. Monthly and biweekly trips of from three to five days were made to the study area throughout that time with the exception of the summer of 1975 when I was doing field work on the study area from June 13 through August 22 for about sixty days. A total of about 125 days were spent in the field during the eighteen months of the study.

The study area was restricted to the area of the University of Minnesota Forestry and Biological Station (SE $\frac{1}{4}$ Sec. 2, T. 143N, R. 36W, Clearwater Co., Minnesota). A map of the study area and the grid system used in this study can be found in Fig. 1. The biology station is different from the surrounding areas of the park (See Hansen et al. (1974) for description of vegetation of Itasca State Park.) by having many open areas and several homogeneous stands of spruce (*Picea* sp.), the cones of which were used by most resident squirrels as their major food source throughout the winter months. Seton (1909) considered one squirrel per three acres (0.823/hectare) as abundant. Klugh (1927) and Hatt (1929) found spruce woods particularly capable of supporting dense red squirrel populations with estimates of two per 100 yards square (2.39/hectare) and 1.8/acre (4.446/hectare) respectively. The relatively high density of squirrels on the study site (1.5 red squirrels per hectare from June 1975 to May 1976) aided the capture and marking of the subjects and enabled me to locate a marked squirrel for observation with little

trouble. Other locations in Itasca Park were inspected for possible additional study sites but none were found where several individual squirrels could be reliably located and trapped. The fact that there was a relatively high density of squirrels on the biology station study area may affect the vocal communication of the squirrels, and the possible increased frequency of occurrence of vocalizations due to increased social encounters aided the recording of the squirrels' repertoir. The vocalizations are otherwise assumed to occur in the same manner and with the same behaviors as would occur in the same but rarer occurrences of social interaction in a less dense population.

Squirrels on the study area were livetrapped using National Live Traps baited with peanut butter and/or sunflower seeds. In the winter of 1974-75 only a portion of the study area was trapped. Fifteen individuals were marked (8 ♂♂, 6 ♀♀, 1 unsexed), released, and recorded in the field. During the summer of 1975 the whole study area was trapped and 31 squirrels were marked (15 ♂♂, including three juveniles; 16 ♀♀, including three juveniles). During the early winter of 1975-76 thirty individuals (10 ♂♂, 19 ♀♀, 1 unsexed) were marked and there were an estimated five to ten additional unmarked residents on the study area. Captured individuals were weighed, sexed, and permanently marked with two numbered ear tags (National Band & Tag Company). Dye-marking for field identification was done with Lady Clairol hair dye (Black Velvet #51) using the number scheme depicted in Fig. 2. Dye applied following the fall or spring molt would last up to six months. All handling of

squirrels after capture was done with a weighing bag and handling cone as described by Halvorson (1972) with the exception that the handling cone wires were not cut to swing open so the squirrels had to back out of the handling cone after processing.

Recordings of squirrel vocalizations were made with and without a 24" Dan Gibson sound parabola on a Uher 4400 Report Stereo recorder with a Sennheiser MD405S microphone, a Uher 4000 Report-L recorder with a Uher M516 microphone, and a Tandberg 11 recorder with a Sennheiser M211U microphone. A Norelco 1420 cassette recorder used for field notes was occasionally used for opportunistic recordings of vocalizations. Low noise, high density cassettes were used for note tapes while 5 inch Ampex 631 Professional reels (1.5 mil polyester backing) were used on the Uher and Tandberg recorders at tape speeds of 3 3/4 and 7½ inches per second. Care was taken not to overload input when recording. Harmonics in spectrograms caused by possible overloading are noted as such.

Data for the Chatter call activity patterns were all collected from the northeast corner of grid location J5 (See Fig. 1.). I noted all Chatter calls heard on a time line as they occurred.

Although territories of the subjects were not rigorously determined during this study, areas of exclusive use, often seen defended from intruders by chasing, were regarded as territories.

Sound Level Measurements

Many vocalizations were directly measured for their volume with a Realistic Music/Sound Level Meter (Range: 60-116 db;

Accuracy: ± 2 db at 114 db sound pressure; RE 0 db = 0.0002 dynes-per-square-cm.; meter ballistic characteristics [(switch selected) set on Fast to ASA standards.] both in the laboratory and the field. Some tapes used for recording vocalizations in the field were calibrated with pre-recorded 0.5 and/or 1.0 kHz sine wave tone bursts (100 ms burst at 4/sec.). The tone bursts were measured with the sound level meter as they were recorded onto the tape to be used for recording vocalizations in the field. This calibration procedure was done in the laboratory at one meter. After field recordings were made, the distance between the squirrel and microphone was noted for each vocalization to be measured. These tapes were later played in the laboratory through the tape recorder's speaker at the previously calibrated level and amplitude was measured by the sound level meter placed one meter from the speaker.

Vocal amplitudes were extremely difficult to gather directly in the field because the limited sensitivity of the sound level meter demanded that a vocalizing squirrel be within three meters of the sound level meter for the needle to register. I was fortunate in trapping some vocal squirrels whose vocalizations could be measured directly in the laboratory. The sound levels measured from the calibrated tapes are suspect since only one calibration distance was used and microphone input rather than line input was used in measuring the recorded vocalizations (due to lack and limitations of equipment). The results from the calibrated tapes have not been excluded from this paper, however, since they do compare well with the direct measurements and it is hoped that by having a

larger number of vocalizations measured and presented that future researchers will be stimulated to advance this important but heretofore neglected aspect of vocal communication of sciurids with more refined techniques. Sound levels measured directly are discussed with the description of the vocalization and presented in Table 1. Measurements from both calibrated tapes and direct measurements are included in Table 2 and discussed in the section on sound level of red squirrel sounds.

Playback Methods

Five different red squirrel vocalizations were selected for playback purposes from the vocalizations recorded from the population. Black-capped chickadee (Parus atricapillas) vocalizations recorded from birds active in the study area served as a control. (See Fig. 4g for sample of chickadee vocalizations used.) In an effort to avoid the possibility of habituation, each playback to a given individual was separated from the next by at least ten days. Sequence of playbacks was randomized (without repetition) for each marked individual for the six different playback tapes. No squirrel was the subject of the complete sequence and no subject heard its own voice on the playback tape. The possibility of hearing the voice of a neighbor on the playback tape occurred only twice, both for the Peep-Chuck sequence playback tape. All eartagged but undyemarked squirrels were treated as a single individual and had a single randomized sequence, thus avoiding repetition. Unmarked squirrels were treated similarly. The distribution of playbacks made is presented in Table 3 and sound pressure levels of the sounds

played back can be found in Table 4.

I attempted playback experiments only while squirrels were feeding or foraging so as to have a relatively standard baseline behavior for comparison purposes. When a squirrel was located for an experiment, a Nagra field speaker/amplifier was hung 0.75-1.5 m up in a tree in the vicinity of the squirrel. No attempt was made to disguise the speaker and I was not in a blind or deliberately hidden except for standing behind a nearby tree. I took a position up to 15 m from the speaker with the Uher 4000 Report-L or Tandberg 11 recorder connected to the speaker by a 15 m coaxial cable. The experiment began by noting the squirrel's behavioral activity (feeding, foraging, movements, vocalizations, etc.), orientation to the speaker, and position on the ground or in a tree for a total of eleven minutes noting changes in behavior as they occurred. Playback of the pre-recorded vocalization occurred during the sixth minute. While the "Peep-Chuck" sequence and the "Chickadee" sequence used for control experiments were both continuous recordings for the full minute, all other playback tapes consisted of a vocal burst lasting from 3.5 to 9.0 seconds (See Table 3.) repeated three times starting at 0, 20, and 40 seconds during the sixth minute. Following an experiment, I measured distances between squirrel and speaker and between squirrel and myself from its position before and after the playback experiment with a steel tape. I also measured the distance from my point of observation to the speaker and noted compass directions. I noted location, position, and the direction the speaker was facing as well as temperature, wind velocity and dir-

ection, and cloud cover, and made a verbal summary of the experiment, problems, and unusual circumstances on the note tape.

Each playback experiment and collected data were recorded on one side of a cassette tape using a Norelco 1420 recorder. The notes of each 11 minute experiment were later transcribed onto a time line, the site of the experiment mapped, and the other pertinent information recorded on a data sheet.

Laboratory Work

Preliminary spectrographic analysis of vocalizations were done on a Kay Vibralyzer 7030A sound spectrograph. Sound spectrograms for a total of about 400 minutes of red squirrel vocalizations were made using a Real Time Analysis system as described by Hopkins et al. (1974). Real time analysis was recorded by continuous filming with a continuous recording oscilloscope camera using a TEAC model 234 stereo tape recorder, or the Uher or Tandberg recorders mentioned above. An analysis range of 10 kHz was used with tape speeds $\frac{1}{4}$ the recorded speed and a 20 kHz analysis range was used when tape speed was set at $\frac{1}{2}$ the recorded speed. Display width was set at 25% giving an effective 3 db bandwidth of 120 Hz. Four and eight kHz frequency calibrations and at least two seconds of 0.5 second time calibrations were made at the time of filming for each sonogram made by real time analysis.

Statistical analysis of the playback experiments was programmed on a Hewlett-Packard HP 9820 programmable desk calculator. Histograms and chi-squared plots were done on an HP 9862A calculator plotter.

RESULTS

In the presentation of the vocalizations recorded in this study each vocalization will be named, a figure reference given, and a short statement made of the most common function as determined in this study. A physical description of the vocalization follows and the reader is urged to refer to the proper figure. A verbal analogy is made for each vocalization so that the sound can be more readily identifiable in the field and the names given to these sounds by previous studies are noted. Sound levels measured directly with a sound level meter are then presented and this is followed by observations of acoustic behavior based on laboratory and field observations. These observations and the accounts presented in Tables 5 through 14 are based on field notes, recordings, and playback experiment records where I had data on the probable cause of a vocalization or information on the effect a vocalization voiced by a squirrel in the field had on the behavior of another. The number of observed cases of each vocalization as presented in Tables 5 - 14 should not be construed to indicate the relative frequency of occurrence of the vocalizations.

Vocalizations

Peeps (Fig. 3a, b, c, d, e). The Peep vocalization is the most frequently used vocalization used by the red squirrel and serves as a low intensity alarm call, but this should not be considered its sole function or interpretation as will be discussed below for the other vocalizations as well.

Peeps typically have an upswing in frequency immediately followed by a downswing, the note lasting from about 0.1 to 0.2 seconds. This vocalization is usually given repeatedly with an internote interval as short as 0.05 seconds or as long as several seconds. The internote interval can vary within a single sequence as seen in Fig. 3a. The Peeps in Fig. 3a have a frequency modulation from 7 kHz up to 8 kHz and then down to about 5 kHz. Also considered as Peeps in this study were three part harmonic Peeps (Fig. 3b, c) and two part harmonic Peeps (Fig. 3d). The variability which occurs in the frequency modulation in Peeps is clear in these examples and I have observed such variability from a single individual as well as between individuals. I have recorded one, two, and three part harmonic Peeps from a single individual during a single recording and simultaneously recorded another individual vocalizing single component Peeps indicating the harmonics are not likely due to input overload.

The Peep vocalizations sound very much like the peeping made by a newly hatched chick. Embry (1970) called the Peep a "Squeak-Whistle" while Smith (1965) merely included it in his "Alarm calls" catagory.

The Peep is not a very loud vocalization. Direct measurements in the field from 6.9 m to as close as 1.3 m failed to register on the meter. Direct measurements made in the laboratory at 0.5 m ranged from 68 to 79 db (See Table 1.).

The vocalizations found to accompany 105 cases of Peep vocalizations are broken down into four situations in Table 5. The Chucks

that occur in the "In Trap" catagory occurred in the laboratory and in one case another squirrel was present. There were two cases when a Growl was also given but these were apparently stimulated by another squirrel outside the captive's trap aggressively responding to the captive. The Growl that occurs under the "Observer" catagory was given in response to a squirrel held in a trap. Considering this, all Growls, Multiple-Chucks, and Whines that occurred in association with Peeps were directed at conspecifics. Peeps not directed at conspecifics (79 cases) constituted 75.2% of the red squirrels' use of this vocalization.

Groan (Fig. 3a). The Groan vocalization is generally used in low intensity alarm situations and occasionally occurs alone but more frequently occurs after a Peep or a Chuck as in Fig. 3a.

The Groan has essentially no variation in its frequency for the 0.2 to 1.0 second duration. This 0.5 to 1.0 kHz vocalization is often given repeatedly, but seldom without an intermediate Peep or Chuck given first.

The Groan vocalization sounds like a short hum and I believe it is this that Klugh (1927) refers to as a low "meur-meur-meur" sound. Smith (1965) and Embry (1970) do not discuss this vocalization, although Embry refers to Klugh's "meur" sound as being the same as her Squeak-Whistle (Peep).

I was unable to make any measurements of the sound level of the Groan in the field or laboratory. This vocalization is subjectively perceived by human ears as being of lesser amplitude than the Peep.

In 23 cases of its use observed in the field the Groan vocalization was always observed to occur with Peeps. (See Table 6.) (The exception of this was in a case where Growls were grading into Groans. These vocalizations were given by an adult female as she passed another squirrel when descending a spruce to the ground.) Fourteen (60.9%) of the cases occurred in response to the observer and nine (39.1%) cases involved conspecifics. The single case of Drumming accompanying the Peeps and Groans occurred in response to the observer.

Chuck (Fig. 3b). The Chuck vocalization serves mainly as an alarm vocalization. The Chuck ranks above the Peep and Groan, but below the Trill in alarm intensity.

The Chuck is composed of a single vocal burst lasting from about 0.05 to 0.1 seconds and generally covers frequencies from 0 to 10 kHz (limits of the spectrum used in this study) and above. This vocalization is repeated often, the repetition rate increasing with the intensity of the alarm and motivational state of the squirrel. The first and last Chucks in Fig. 3b demonstrate how a Peep vocalization can immediately precede the short, broad band Chuck. This close temporal relationship between the Peep and Chuck is not uncommon in the squirrels' use of these vocalizations and Embry (1970) called such a composite a "Chee" note and designated the Peep as the alpha component and the broad frequency band as the beta component. Since it is difficult at times in the field to distinguish between a Chuck and a Peep-Chuck composite, I have adopted her use of these component names when differentiating

between the components of such a vocalization.

A single Chuck vocalization sounds like an abbreviated bark of a very small dog. Smith (1965) includes this vocalization in his "Alarm calls" catagory while Embry (1970) calls it a component of the "Chee" note. It is interesting to note that Embry regards the alpha component and the Squeak-Whistle (Peep) as separate and distinct, yet the spectrograms made indicate they are not spectrally different. The internote interval between alpha (Peep) and beta (Chuck) components can be highly variable as indicated in Fig. 3b. Searing (1975, 1977) calls this vocalization a "Bark" and argues that it serves as a weak aggressive call.

I was unable to get a reading for the decibel level of Chucks in the field even from as close as 2.4 m. In the laboratory Chucks ranged from 80 to 85 db at 0.5 m and were generally from 5 to 10 db louder than the accompanying Peep vocalizations. (See Table 3.)

In observing 54 cases of the vocalization used once or more in nature (See Table 7.) Chucks directed at the observer were always accompanied by Peeps except for once in the field and three times in the laboratory. In two lab situations the squirrels gave Chucks while being handled and chattered their teeth when returned to the live trap. On the one occasion indicating that a Growl was directed at the observer another squirrel was present and was the likely stimulus for that vocalization. Generally, Chucks accompanied by Growls or Multiple-Chucks were directed at another squirrel while Chucks accompanied by a Trill were directed at the observer.

Trill (Fig. 3c, d, e). The Trill vocalization is a high

intensity alarm call nearly always given as the vocalizing squirrel is running or climbing away from an immediate potential danger.

The Trill is usually composed of three to five Peep vocalizations given in rapid succession in a single exhalation by the squirrel and is accompanied by a crackling sound produced by the squirrel's claws as it rapidly moves along a tree trunk or branch. I have never observed this vocalization to occur without an accompanying rapid movement although I have observed the rapid ascent of a squirrel and the accompanying mechanical noise without hearing the vocalization. Figure 3d shows separately both a Trill accompanied by this rapid ascent noise and the rapid ascent noise alone without the vocalizations. Notes of the Chuck vocalization are often incorporated into the Trill which lasts from about 0.5 to 1.5 seconds. The Trill is commonly given following a series of Peeps as indicated in Fig. 3e. Trills are at times given more than once if the disturbing stimulus remains present or renews its threat, but are never heard as frequently as Peeps or Chucks.

The Trill vocalization sounds like a loud and excited, closely sequenced series of Peeps and/or Chucks. Embry (1970) did not deal directly with this vocalization in her study. Smith (1965) presents a trilled note from a hybrid (T. hudsonicus and T. douglasii) but it is included with several other vocalizations and simply referred to as a note from an alarm call. Searing (1975, 1977) refers to this vocalization as a "rapid squeak" given as a squirrel is running from a predator.

The Trill vocalization sounds relatively loud and I have

measured it in the field from 3.0 to 3.5 m at 64.5 db (See Table 3.). When occurring with Peeps, Groans, and Chucks in an alarm display, the Trill is usually marked in its loudness but may be no louder than the more vigorous Chucks and at times may be quite muted in amplitude but readily recognized by the abrupt rapid movement that accompanies it.

The Trill vocalization (See Table 8.) occurred in 21 of the 30 observed cases (70.0%) in response to my presence. In an additional two cases when a captive squirrel was held in a free squirrel's territory or a free squirrel vocalized the Trill upon a captive's release, my presence was probably the stimulus. In all these cases the squirrels would typically be vocalizing Peeps (occasionally Chucks and Groans as well) at me and give a Trill as they rapidly ascended about 1.5 m up the tree trunk or along a branch where they would continue Peeping. Three cases were observed when a distant Trill caused subjects being watched to alter their behavior, ranging from raising their head from feeding and looking around, to flinching at the sound of the vocalization, perking up into a more erected posture and becoming alert. In one case when my presence caused a Trill from one squirrel, another nearby squirrel immediately ceased its feeding on the ground, ran to a tree and paused, alert, at the base of the trunk.

On one occasion in April 1976 a marked squirrel gave a Trill as it was being chased by another squirrel. An unmarked squirrel on the ground nearby, alert to the chasing squirrels, climbed up a tree in response to the Trill vocalization, and there maintained

its alertness.

In early May 1976 I was observing an unmarked squirrel near the top of a spruce when I heard a flutter of wings there. The squirrel gave a Trill, rapidly descending the tree to the lower branches, and commenced vocalizing Peeps. Soon after, a crow (Corvus brachyrhynchos), believed to have a nest in the tree, gave a couple "wah" calls. It should be noted that the squirrel gave the Trill as it descended, moving away from the crow which may have been regarded as a predator. All Trills observed in response to me have been associated with a rapid ascent, but again away from the potential danger.

On 19 December 1975 I observed a juvenile female give a Trill and run up and down between three and six meters up in a cedar as if being chased or chasing. No other squirrels were in the vicinity and I'm quite certain that the squirrel was not aware of my presence during this display of solitary play. This play activity would fit into Ferron's (1975) "Leaps and Feats of Skill in Trees" catagory of Non-directed Solitary Behavior in red squirrels. Ferron made no mention of vocalizations associated with any instances of solitary play he observed.

Scream (Fig. 3f). The Scream vocalization is a physical contact alarm call as opposed to the Peep, Groan, Chuck, and Trill which are visual contact alarm vocalizations.

The Scream is composed of a series of three or more notes with a relatively constant internote interval of about 0.15 secs. Each note has an upswing from 0 to 2 kHz and then returns to 0 kHz, the

note lasting about 0.1 seconds. The harmonics seen in Fig. 3f are possibly due to an input overload, but the 1 to 2 kHz band of noise in the "internote" interval is a real component of the vocalization. All the Screams I recorded in the laboratory had a starting and finishing note that looks and sounds like a Growl note.

Though the Scream has a 2 kHz fundamental frequency, this vocalization sounds like a series of high pitched, piercing, shrill screams. The Scream has been described by Dice (1921) and Klugh (1927) but I believe this is the first spectrographic presentation of this vocalization. Embry (1970) did not describe this call and Smith (1965) only mentioned the past accounts from the literature.

Two cases of the Scream vocalization were recorded in the laboratory, once from a male and once from a female. In both cases the squirrel made the vocalizations while being handled in the handling cone or weighing bag. Neither squirrel appeared to be adversely affected by the handling which was no different than that received by other squirrels in the marking process.

The Scream was heard once in the field when two squirrels were having a vocal altercation high in a tree out of sight. During a portion of the vocalizations one of the squirrels gave several intense Screams which graded from a series of Growls.

Chatter (Fig. 3g). The Chatter (or "chirring") vocalization is a loud call that largely serves as a territorial announcement.

This vocalization varies in length from less than a second to several seconds and is composed of notes of very broad frequency range given at twelve to thirteen per second at the beginning of

the vocalization and commonly slowing down to a slower repetition rate at the end of the vocalization. I have recorded the Chatter from a single breath to last up to thirteen seconds. This vocalization is usually heard singly but occasionally several Chatters will be given in close succession.

The Chatter sounds much like the sound produced by man when we vibrate our tongues rapidly by forcing air over them. Embry (1970) uses this analogy and calls this vocalization the "Rolled-R" call. Smith (1965) designated it the "Territorial call" and it is frequently referred to in the early literature as a "chirring" sound. Searing (1975, 1977) interprets the territorial announcement as being an aggressive vocalization.

A red squirrel will commonly throw its head back and open its mouth wide when making this vocalization. The one measurement of amplitude I was able to make directly in the field of a Chatter registered 64 db at 3.0 meters (See Table 1.).

The Whine vocalization was heard just before or just after a Chatter in about 20% of the observed cases of the Chatter. In two situations not included in Table 9A, Whines accompanied nearly all of the Chatters that occurred. In one case an individual gave Chatters and Whines at a displaced opponent after a long and intense interaction over a territory. The vocalizing squirrel paused only briefly in a solid minute of several Whine series and Chatters. The other case was also a boundary interaction where an adult female used Peep, Chuck, and Growl vocalizations while an adult male used Whines and Chatters throughout the seven minute encounter.

Chatters are frequently given when there is no apparent stimulus from other squirrels, and often just the sound of a distant squirrel vocalizing is sufficient to trigger a Chatter (See Table 9B). I have observed a squirrel give a Chatter upon becoming active in the early morning and it is not uncommon to hear one squirrel's Chatter being answered by that of another. The intrusion into a territorial squirrel's area by a human or another squirrel is often sufficient stimulus for a Chatter and when the Chatter is accompanied by Whines and directed at an intruding squirrel, the intruder will almost certainly be displaced. The Chatters given by males during mating chases were most often directed at other males in pursuit of the same female.

On one occasion a squirrel that was foraging outside of its territory was disturbed by my presence. It returned to its territory across a path, directed a Chatter at me, and returned to the area it was in and resumed foraging. It was not unusual to observe Chatter calls from squirrels that were chased back into their own area after intruding in another's territory - but the intruder's Chatter was not likely to occur until after it had crossed into its own territory.

The Chatter was the only vocalization used by the red squirrel by which I could distinguish between individuals based on voice alone, and this was limited to only two or three individuals. There were peculiarities of tonal quality in the Chatter of those few individuals so that I would not have to see them to know their identity if they voiced a Chatter. Unfortunately I was unable to

record these vocalizations to determine what the spectral differences were and I have no data on individual recognition by the squirrels based on voice, but would not be surprised to find out that this does occur. Individual call recognition experiments done by Searing (1975) were conducted using three Chatters played at 10 minute intervals in one of two sequences: either Neighbor-Stranger-Neighbor or Stranger-Neighbor-Stranger. Subject squirrels responded to the first played call more often than the second regardless of whether a neighbor or stranger and there was no statistically significant difference in intensity of response with respect to whether that first call was of a neighbor or stranger. Searing also could find no physical parameters in the sample of 27 Chatters from fourteen squirrels that could serve as the basis of individual recognition.

The occurrence of Chatters, measured for two to four days in August 1975, indicates a peak "morning chorus" to occur about fifteen minutes before sunrise (See Fig. 14.). The Chatters stay at a relatively high level in the early morning and then drop off to a lower level which is maintained throughout the day. There is a slight increase again for about twenty minutes following sunset. This Chatter activity pattern closely parallels the activity pattern of red squirrels based on counted squirrels as reported by Layne (1954).

Whines (Fig. 3h). The Whine is a vocalization of aggressive intent and is used frequently in situations where an intruding squirrel is displaced.

The Whine is characteristically composed of a frequency modulated fundamental note lasting up to a second with two to six or more harmonics. A single Whine vocalization can be composed of several of these notes each separated by a 0.1 second or longer interval of silence, and such a series of notes is commonly given in a single breath. The Whine vocalization is often heard immediately following a Chatter (See Table 9.).

The Whine sounds like a small dog whimpering and is called a Squeak by Embry (1970), a Loud Aggressive Call by Smith (1965), and a "Tsew" by Searing (1975).

I was unable to make direct measurements of the sound level of the Whine in the field but it can be clearly heard from 100 m and is often heard in the distance following a Chatter.

In all twenty cases where a Whine occurred without a Chatter (See Table 10.) a specific squirrel was the target of the vocalization and nine times (45%) the vocal target was displaced. (In one instance both Whines and Growls were used to displace the target squirrel.) In the three cases where a squirrel that gave Whines had just been displaced it is known that at least one of the squirrels gave its Whines only after it had returned to its own territory.

Multiple-Chuck (Fig. 4a, b). The Multiple-Chuck is a vocalization of aggressive intent usually given when an intruder is coming into or has already entered the territory of the vocalizing squirrel.

The Multiple-Chuck vocalization is a series of Chucks (each

composed of an alpha and beta component or beta components alone) produced in a single breath each immediately following the preceding note. They usually occur with Chucks, Peeps, and/or Growls and were always seen directed at another squirrel. The Chucks and Peeps that are associated with the Multiple-Chucks are also directed at the target squirrel so in this context the Peeps and Chucks are probably components of an aggressive display.

The Multiple-Chuck sounds like a very rapidly produced series of Chuck vocalizations and are regarded as a trilled "Chee" call by Embry (1970). I believe Smith (1965) would regard this vocalization as another of the many components of his "Alarm calls" catagory, but this study indicates that the function is probably otherwise.

I made no direct measurements of sound level of the Multiple-Chuck but it is safe to say that it would be in the range of the Chuck's amplitude. Squirrels that voiced a Multiple-Chuck appeared to be in an excited state and accompanying Chucks sounded loud so the Multiple-Chuck may have a higher average sound level than the Chuck.

The Multiple-Chuck vocalizations presented in Table 11 were directed at conspecifics in all observations and in six (50%) of these cases the squirrels vocalized at were displaced. In two instances the squirrel that gave the Multiple-Chuck was displaced. In one of these cases a female re-entered a contested area from which she was displaced earlier. She gave a Multiple-Chuck vocalization as she entered the area but the female that was in the area

approached the intruder vocalizing a series of about 25 Whines and the intruder was again displaced out of the area. Whines do not necessarily indicate dominance over Multiple-Chucks, however, since on a different occasion, an unmarked squirrel gave Whines while moving out of an area chased by an eartagged squirrel which gave Multiple-Chucks.

Growl (Figs. 4c, 5e, 6d). The Growl vocalization is an aggressive vocalization given during an immediate encounter with another squirrel and can vary from a couple short muted notes to a long and loud series of notes.

The Growl is a broad frequency band raspy sounding vocalization (ranging from 0 to about 6 kHz and going as high as 9 kHz, but generally not much frequency modulation within any given note) with notes of one second or less in duration given in a series with internote intervals varying from less than 0.1 second to over 1.0 second.

A single Growl note sounds like a short growl from a small dog. Embry (1970) also calls this sound a "Growl" but Smith (1965) designates it as a "Quiet Aggressive call" characterized by its growling sound.

The sound levels of two sequences of Growl notes (See Table 1.) measured at 0.3 m in the laboratory ranged from 64 to 68 db. In the field a tremendous variability of volume can be heard when the Growl is given in an aggressive encounter. The fact that Smith (1965) regarded the Growl as a "Quiet Aggressive call" indicates the fact that this vocalization can be quite muted, but in an

excited state a red squirrel can and does give this vocalization very loudly, even as loud as the "Loud Aggressive call" (Whine).

The Growl vocalization (See Table 12.) was directed at a human observer only twice (3.8%). In one case, Chuckles which graded into Growls were elicited from a captive adult female by blowing on her. She actively struck out with her paws, hitting the trap sides at my blowing. In the second case on 22 August 1975 I came across a very small juvenile that must have just recently left the nest. The young squirrel was seen running across a road and it stopped on the ground as I drew near. It allowed me to approach and touch it but when I tugged on its tail a little, the squirrel rolled over onto its back and vocalized aggressively giving Growls and pawing the air as if boxing. I have seen similar postural and motor reactions by adults that were in lengthy physical contact while fighting for a food cache.

The Growl directed at conspecifics occurred when two or more squirrels were in immediate proximity to one another and were often given by both squirrels as they faced off. Of the fifty intraspecific cases when the Growl was used, displacement occurred in 22 (44%) cases and in fifteen of these 22 cases the Growl was unaccompanied by other vocalizations. In an additional eleven cases Growls were given at a squirrel held in a trap so displacement could not occur. It was not unusual for the free squirrel to attack the caged squirrel in these situations. On only one occasion was a squirrel heard to give Growls immediately after being displaced. (Growls did occur commonly after a displacement if another confron-

tation was about to occur.) An estrous female was seen to displace with Growls males she was unreceptive to on at least three occasions.

Some of the Groans and both Chuckles indicated in Table 12 are the result of Growls grading into these types of vocalization.

Chuckle (Fig. 6d, e, f). The Chuckle is a quiet vocalization that indicates aggressive intent and is used in close, immediate encounters. The Chuckle is actually a series of very shortened Growl notes but since the perceived sound to man is quite different from the Growl, I have chosen to deal with it separately.

Each note of a Chuckle can be as short as 0.02 seconds long with an internote interval of 0.05 to 0.5 seconds. The notes of a Chuckle can have a high frequency as low as about 2 kHz or as high as 9 to 10 kHz.

The Chuckle sounds much like the rapidly repeated sound of the letter "t". Neither Embry (1970) nor Smith (1965) made any reference to this vocalization.

Chuckles given by a squirrel in the laboratory at 0.2 m from the microphone failed to register above the 60 db limit of sensitivity on the meter. Chuckles given in the field may be less inhibited and therefore louder, but the Chuckles heard in the field were still very soft and difficult to record.

The Chuckle vocalization was given in the lab on two separate occasions by different squirrels. In both cases the squirrel aggressively struck the sides of the trap and gave the Chuckle vocalization in response to my gloved hand or my blowing on the squirrel.

In one of these cases Chuckle notes graded into Growls. On two occasions recorded in the field, Chuckles which graded from Growls were given by a squirrel in response to another squirrel which had approached closely. No displacement occurred in either case. In an additional case, one of two squirrels in a chase gave a Chuckle vocalization but which one is unknown.

Buzz (Fig. 4e). The Buzz serves as an appeasement call used by juveniles and also by adult males during the breeding season when trying to gain access to an estrous female.

The Buzz is generally of low amplitude and can sound quite nasal in tonal quality. Each buzz note lasts from about 0.1 to 0.25 seconds and I have recorded them occurring as rapidly as four per second but an internote interval of 0.5 to 1.0 seconds is more common. Both Smith (1965) and Embry (1970) present sonograms of this vocalization which indicate that it has a low frequency component from 0 to 1 kHz and a higher frequency component at about the 6 kHz range. The Buzzes I recorded were made with the Norelco 1420 recorder without a parabola so these weak recordings do not show any higher frequency components should they be present.

The Buzz sounds very much like the sound one can produce by making a low pitch hum while simultaneously making the sound of the letter "z" and directing the major portion of exhaled air through the nose. The Buzz is called the "Appeasing call" by Smith (1965) and "Juvenile Sounds" by Embry (1970). Smith notes that this call can be differentiated by its low frequency voiced fricative buzzing sound.

No sound level measurements were made of the Buzz. It was much softer in loudness than the Peep but may be comparable with the Groan in amplitude.

Behaviors accompanying the Buzz vocalization were observed largely during the first breeding season of 1976 (March - April). In only two instances were Buzz vocalizations positively identified as coming from a female. On one of these occasions an adult female gave the vocalization in displacing a male who had entered her territory. She was not believed to be in estrus at the time. The only other occasion a female was heard to give a Buzz was when an estrous female alternately made Buzzes with a courting male.

In eight cases the Buzzes were directed at other males, in six cases at an estrous female, and in four cases at both the other male(s) and the estrous female in separate series of Buzzes (See Table 13). In four cases the sexes of the squirrels were not determinable. Most of the observed cases of the Buzz occurred during mating chases where males would run upwind toward the estrous female, often with their noses to the ground where she had passed, vocalizing series of Buzzes even before the female was within their sight. When the female was sighted, Buzzes would be given as the male approached her closely. The Chatters which occurred in association with the Buzzes were commonly given by a male in company with an estrous female upon the approach of another male, but Chatters were also directed at the female. A female also gave Chatters during one of the mating chases observed but females used the Growl in displacing males to which they were not receptive.

Squeak (Fig. 4d). The Squeak is a soft, high pitched peep ranging from about seven to ten kHz with each note (0.2 - 0.4 sec.) lasting from two to three times as long as a single Peep note. This vocalization was made by a squirrel in the lab as it was being handled and may serve as a type of distress vocalization or as an indication of discomfort. I made no sound level measurements on this vocalization. It was the quietest vocalization I have heard made, softer than the Buzz or even the Chuckle. Smith (1965) and Embry (1970) make no mention of this vocalization and I heard and recorded it on only the one occasion.

Non-vocal Acoustic Sounds

Drumming (Fig. 4f). Drumming is the repeated movement of alternately raising and lowering the hind or forefeet against the substrate which thereby produces a sound. The frequency of the foot taps ranges from about seven to 25 taps per second. Drumming is usually seen to occur with Peeps and Groans in an alarm display but I have seen it used in other contexts as well.

Drumming was observed in the field in response to the observer on five occasions and in all of these cases the Drumming was accompanied by Peep vocalizations. Drumming was elicited from two squirrels in the laboratory by drumming the index finger of each hand rapidly for one to two seconds on the table next to the captive's trap and then pausing before repeating. The squirrel would drum at the pause, and one squirrel made a Peep vocalization at each pause in my drumming.

Drumming in response to a conspecific was seen on two occasions in the field. Drumming accompanied a vigorous vocal and physical attack by an unmarked squirrel on a captive squirrel placed in the unmarked squirrel's territory. The only case observed where a subject drummed all four paws occurred when a male had approached an estrous female. His drumming occurred with Buzz vocalizations and his tail wagged back and forth in the leaves on the ground. Generally the red squirrels observed would drum their hind paws when positioned upright along a vertical branch, when on the ground, or on a horizontal branch. Drumming of the forepaws was seen in at least one squirrel as it was hanging by its hindpaws on a tree trunk.

Substrate Scratching and Rapid Ascent. The non-vocal acoustic sound of the red squirrel's claws scratching along the bark of a tree does serve in acoustic communication. All Trill vocalizations observed in this study were accompanied by a rapid movement which, when made in a tree, produced a considerable noise. The fact that these squirrels can move quickly and silently through the trees indicates that the scratching sound is not just incidental. The scratching sound of a rapid ascent has been recorded unaccompanied by any vocal utterance (See Fig. 3d.) and, though not as loud as the vocalization, does contribute to the quality of sound produced in the Trill. The scratching sound of the squirrels' nails is also used in situations where the squirrel makes short, jerky hops along a branch giving Peep vocalizations in mild alarm (See Fig. 6g, h.).

Teeth Chattering. Teeth Chattering was observed in three instances from two individuals but only in the laboratory. Both squirrels made the faintly audible chattering from inside the trap after having been handled. The jaw of the squirrel could be plainly seen to quiver rapidly as they produced the chattering. I have no information of whether the sound would be any louder in the field under different circumstances but it would nevertheless serve only in very short range acoustic communication.

Tail Movements Accompanying Acoustical Communication

Small tail-flicks often accompany each Peep or Chuck in an alarm situation and the tail is often held erect while escaping from another squirrel. An unmarked squirrel active in some tree branches moved its tail rapidly up and down and laterally (whipping it in a circle) as it gave Groans and drummed its hind feet during a Peep-Groan sequence responding to my presence. In December of 1975 an eartagged squirrel on the ground gave a series of Growls and wagged its tail back and forth sideways as another squirrel approached right up to it and past. On two occasions different males were seen to wag their tails back and forth in the leaves on the ground after they had approached closely to an estrous female. In these cases the tail movement itself caused a sound.

Vocal Behavior upon Release from Captivity

It was noticed early in this study that live trapped squirrels would frequently vocalize a Chatter upon their release or soon after

the observer left the release site. Data collected based on this observation are presented in Table 14. In three instances when a Chatter was not given (Table 14B) another squirrel in the vicinity gave Whine vocalizations and/or attacked the released squirrel. In three cases where the released squirrel gave a Chatter, neighbor squirrels gave a Chatter in answer, and in one case another squirrel in the vicinity of the released squirrel responded aggressively (vocally and physically) to the released individual's Chatter.

On two separate occasions with two different subjects, upon release, after having been held for an hour or more, the squirrel moved throughout its territory giving many Chatter vocalizations. No other squirrels were in the immediate vicinity when these vocalizations were made.

Sound Levels of Red Squirrel Sounds

The sound pressure level of red squirrel sounds measured in this study are summarized in Table 2. The sample size of most of the sounds is very restricted but is adequate for comparisons to be made. Laboratory readings were found to be from two to five decibels louder than field readings for the calibrated playback tapes (probably due to the acoustical properties of the laboratory). All data for all orientations of the squirrels to the microphone are combined in the table without regard to the obvious effect this may have on the sound levels recorded.

Data on the Groan, Multiple-Chuck, and Buzz vocalizations were not obtained. The Groan sounds softer than the Peep but the fact

that it is also a much lower frequency than the Peep may cause a perceptual bias in guessing its relative sound level. The Buzz is believed to be softer than Peeps but here again the different structure and frequency of the vocalization may bias human perception. On a calm day I could hear the Buzz given by squirrels up to about fifty meters away.

Drumming is included in the table to indicate that this behavior can have significant acoustic properties. It must be pointed out, however, that the sound level of Drumming listed in the table is from a captive squirrel drumming inside a metal trap, the trap helping to produce a possibly louder sound than is usually heard when a red squirrel drums on a trunk or branch.

Graded Nature of Vocalizations

A gradation from one vocal type to another is often apparent in the real time analysis spectrograms for some vocalizations. Smith (1965) noted that "it is likely that there is a continuum between loud (Whines) and quiet (Growls) aggressive calls, but it is seldom evident." Figure 5a demonstrates this continuum between these vocalizations showing Whines grading into Growls. Figure 5b shows some of the variation in note length and composition that can occur in a single series of Whines. Figure 5c demonstrates how two separate Peep notes can be temporally joined to form a single note which can vary tremendously from the "typical" Peep shown in Fig. 3a.

The beta-Chuck can be seen to grade into a short Growl in Fig. 5d, and Fig. 5e shows gradations of Growls into Groans. Very

short duration Growl notes in Fig. 6a grade into a repetition of these Growl notes that have a temporal and frequency pattern nearly identical with the Chatter, yet are given at a lower amplitude than is commonly used with the Chatter and so, in fact, sound like a rapid series of short Growl notes and not the Chatter. Figures 6b and c demonstrate how the Growl and Scream intergrade. The Growl vocalization is composed of notes of various durations and as these notes become shorter and shorter as seen in Figs. 6d, e, and f, the sound produced becomes a low, rapid clicking which is the Chuckle.

Figures 6g, h, and i demonstrate how the scratching of a squirrel's nails on tree bark can affect the sound quality of vocalizations other than the Trill. The bark scratching following the Peeps in Fig. 6h produce a pseudo-Chuck, the tonal qualities being easily distinguishable from a true alpha-beta Chuck. The scratching sounds accompanying the Peeps in Fig. 6i were made as the vocalizing squirrel made a stiff-legged hop with each Peep.

Playback Experiments

The results of the playback (PB) experiments are presented as histograms in Figs. 7-12. "Alertness" in Figs. 7-12 was characterized by cessation of other activity, erected posture, ears perked up, and fixed gaze. Orientation toward the speaker was scored if the squirrel was facing within 45° of the speaker location. Chi-squared tests were conducted to test whether there were significant changes in behavior between pre-PB, PB, and post-PB periods within

each experiment and were run on each of five intervals, three to eleven minutes in length, with the number of pre-PB and post-PB minutes being equal (i.e. three minute interval includes minutes 5, 6, and 7; the five minute interval includes minutes 4, 5, 6, 7, and 8; etc.). If no response occurred to a PB, the squirrel's behavior was expected to be statistically the same for pre-PB, PB, and post-PB periods. The average frequency of behaviors per squirrel for the interval tested was used for the expected value in calculating chi-squared. The horizontal line at 5.99 in all of the graphs in Fig. 13 is the X^2 acceptance level for $X^2_{.05}$ (d.f. = 2) (Siegel, 1956). Points above that line cause a rejection of the null hypothesis that frequency of behavior is the same for pre-PB, PB, and post-PB periods.

Peep-Chuck (Fig. 7). There was a very high increase in alertness during the minute of playback of the Peep-Chuck sequence. The squirrels would generally enter a tree during the PB minute or in the next two minutes, but this response would decay with time, the squirrels gradually returning to the ground. Although Fig. 7 indicates a general increase in Peep vocalizations and orientation toward the speaker, these reaction frequencies were not significantly different from pre-PB levels.

When data from the two experiments where the subject squirrels were hearing a neighbor's voice on the playback tape are excluded from analysis, "Seconds Alert" and "Seconds in Tree" remain significant for all intervals but "Seconds Oriented Toward Speaker" becomes significant for the three, five, and seven minute intervals.

The number of Peep vocalizations were sufficient to apply the X^2 test only to the three minute interval which remains insignificant.

When just the two experiments where the subject squirrels were hearing a neighbor's voice were analyzed, there was insufficient data to apply the X^2 test to the "Seconds Alert" catagory. "Seconds in Tree" remains significant for all intervals, and "Number of Peep Vocalizations" is significant where the X^2 test can be applied (i.e. the three, five, and nine minute intervals). "Seconds Oriented Toward Speaker" are again significant for the three, five, and seven minute intervals but here the significance is due to a marked decrease in orientation toward the speaker during the minute of playback.

Trill (Fig. 8). There is an increase in alertness following the PB of the Trill vocalization which is significant for all intervals. The increase in Peep vocalizations is also significant for all intervals where X^2 could be applied. (Data is insufficient in the three minute interval for X^2 to be meaningfully applied. See Siegel, 1956.) The increased orientation toward the speaker during and after PB are statistically significant for all but the three minute interval. This playback had a sample size of only two experiments and both subject squirrels were in a tree at the outset of the PB and remained in the tree throughout most of the experiment. The Trill PB was omitted on all squirrels as of 8 April 1976 so that the other vocalizations being used for PB experiments would get a better sample size in the remaining time available in the field.

Whine (Fig. 9). There is a significant increase in alertness,

orientation towards the speaker, and Peep vocalizations for all intervals following the PB of the Whine vocalizations. The increased time in a tree evident in Fig. 9 is not statistically significant for any interval, due in part to the high average time spent in a tree in the pre-PB period.

Chatter (Fig. 10). The only statistically significant change in quantified behaviors to a PB of the Chatter occurs in orientation toward the speaker. The slight increase in alertness is not significant and there is quite clearly no movement into a tree. Data on Peep vocalizations are not adequate to apply the X^2 test.

Scream (Fig. 11). When the Scream was played back, the subject squirrel typically became alert at the sound of the PB and immediately ascended a tree and froze in position. These results are clearly evident in the histograms presented. The squirrels would often freeze in position on a branch on the opposite side of the trunk from the speaker after ascending. This fact accounts for the non-significant orientation toward the speaker. All Peeps for minutes nine and eleven occurred during one experiment. That same experiment accounts for 97% of the Peeps in minute ten and 76% in minute eight. The male subject that made these vocalizations was in a tree throughout most of the pre-PB period (53 secs/min., ave.) as well as all of the post-PB.

Chickadees (Fig. 12). There are no statistically significant differences in alertness and orientation for the pre-PB, PB, and post-PB periods when Chickadee vocalizations were played back to squirrels. All the Peeps for minutes seven and eight occurred during

one experiment when the subject squirrel was particularly disturbed by my presence. If those data were removed, there would be insufficient Peep vocalizations to even apply the X^2 test. The reason for the significant response of moving into a tree is unknown and the lack of any changes in alertness and orientation to the speaker further complicates interpretation. The fact that there was no movement into a tree for playbacks of some squirrel vocalizations indicates that these results are not an artifact caused by the methods used. If the Chickadee vocalizations used serve an alarm function, it is possible the squirrels are keying in on the information present in their environment and responding adaptively. Figure 4g is a spectrogram of a portion of the Chickadee (Parus atricapillus) vocalizations used for playback experiments in this study.

DISCUSSION

Based on field and laboratory observations, playback experiments, and the published literature, I have constructed Table 14 as a general interpretation of the most common function of each red squirrel vocalization reported in this paper. It must be pointed out that the functional catagories listed are not absolutes and that some of the vocalizations are used both inter- and intra-specifically depending on the contextual situation. The graded nature of many of the squirrels' sounds further complicates interpretation but Table 15 can serve as a starting point from which special circumstances and other uses of the various vocalizations can be analyzed and interpreted. Since I have attempted to define the vocalizations functionally, the Multiple-Chuck has not been placed with the visual-contact alarm vocalizations as would be done if the vocalizations were classified solely on the basis of physical parameters.

The visual contact alarm calls are highly graded in indicating the level of excitement of the vocalizing squirrel. The Peep grades in volume and repetition rate as does the Chuck. An increase in intensity is further indicated visually by the addition of the tail flick and Drumming. The Trill also grades in volume and repetition rate depending on the strength of the stimulus. Running with the tail erect during the Trill may serve as an additional visual indicator of alarm. The Groan is generally found appended to a Peep or Chuck as an alarm response becomes more intense. Even though the Groan is a quiet vocalization compared to its accompanying Peeps and/or Chucks, it is placed after the Peep in the chart because of

the more common occurrence of the Peep as the initial, low level alarm vocalization.

To quote Farentinos (1974), "Sciurids and mammals in general use a wide variety of olfactory, tactile, auditory, and visual cues in their social communication. In most cases the signalling behavior of an individual includes the simultaneous use of several sensory modalities, the stimulus value of which may vary with the environmental context and the motivational states of the sender(s) and receiver(s)." It is easy to itemize and artificially catagorize various aspects of social communication (e.g. vocal, visual, olfactory, and tactile modes) and this is at times beneficial, but it must be kept in mind that it is through all the channels of communication employed that the intended information is transferred. Though the simultaneous use of different modes may merely be a form of redundancy to assure the transmission of the signal, premature assumption of this may well lead to faulty interpretations of the function of merely a component of the total signal. In fact, much of the communication in the species covered in this paper is of a graded nature, and the gradation of components and the addition of new modes is important in conveying intensity of response to a given situation. "The meaning of the signals seems to depend in large part upon the environmental situation in which they are given and received. This is most evident in the alarm display of squirrels, which is given in response to conspecifics as well as to predators and inanimate objects" (Farentinos, 1974). The vocal signal given in response to a conspecific Sciurus aberti does not produce the

flight to safety by other squirrels that the same signal would cause if directed at a predator. The tassel-eared squirrels do not exhibit differential responses to ground and avian predators, either. A similar predator response was found for the red squirrel in this study and this pattern may be generally applicable to tree squirrels but does not hold for all sciurids since Balph and Balph (1966), for example, have described distinctly different alarm behaviors by the Uinta ground squirrel for avian and ground predators.

The gradations of vocalizations which occur in the red squirrel occur in other sciurids according to Horwich (1972) who states "squirrels show discrete vocalization units which seem to grade into one another, the difference being in the communicatory sub-system involved. Squirrels have a need for an extensive alarm system."

The visual contact "alarm" vocalizations (See Table 15.) in the red squirrel are the Peep, Groan, Chuck, and Trill vocalizations. (I have put alarm in quotes here to indicate that these vocalizations are also given in response to conspecifics and some workers would not consider them alarm calls in that context.) Each of these vocalizations can be used alone but more commonly they are used in association with one another where the addition or move to the next vocalization indicates an increased level of excitement in the squirrel. Gradation is also present in the loudness of the visual contact alarm vocalizations in their range and average peak decibel level. The Peeps averaged 65.5 db (range 53.5 - 72.0 db, N = 242) in the lab while the Chucks that accompanied them were always at least 8.5 decibels louder, averaging 75.0 db (range 66.5 -79.0 db,

N = 35). The Trills measured were louder yet (average 78.0 db, N =3) and one Trill, measured in the field at 85.0 db was the loudest vocalization measured in this study. The results of the playback experiments (Figs. 7 and 8) corroborate well with the designation of these vocalizations as serving an alarm function. Alertness at the time of playback is what would be expected of a squirrel hearing an alarm given in its proximity. An escape into or remaining in a tree where it would be safer from predators was also a response given by the subject squirrels. Vocalizing alarm calls themselves following their retreat into a tree was seen to occur following playbacks and this behavior will be further discussed below in terms of "altruism".

Horwich (1972) notes that tail waving in the eastern grey squirrel serves in alarm displays. Farentinos (1974) discusses the performance of a number of independently variable, highly graded behaviors in the alarm displays (which he says are the most common form of communicative behavior observed) in the tassel-eared squirrel. The continuum starts with a tail fluffing in response to novel or potentially dangerous stimuli. Higher levels of excitement cause the addition of behaviors rather than the displacement of old ones. The next level of alarm response is a repeated antero-posterior tail flicking. The degree of flicking is highly graded, the intensity dependent on the nature of the threatening stimulus and the squirrel's state of excitement. The next level of intensity adds forefoot thumping, or drumming, to the display. This addition adds an acoustic as well as visual component to the display as the paws

striking dry bark of a pine limb produce a crackling sound. After tail flicking and drumming reach a high repetition rate, vocal barking begins. This is the highest intensity alarm level and the rapidity that series of barks are given again varies with the alarm state of the squirrel. The red squirrel utilizes vocalizations at the start of the continuum with additional vocalizations added with increased excitement.

Farentinos breaks alarm displays into two contextual settings, both of which involve threat evoking stimuli. The first is a confrontation with some type of real or apparent danger such as a predator, human, or even a novel inanimate object. It is under this first context that squirrels of the genus Tamiasciurus will often respond to a territorial intruder. The second is in connection with the reproductive activity of mating bouts where the dominant male performs an alarm display to other males when he's next to an estrous female. The red squirrel uses the "alarm" and "territorial" vocalizations in these situations. On some occasions (though rarely) the dominant male will give the "alarm" display to the female he's courting - and in the red squirrel this also holds true for the Chatter.

Embry (1970) indicates that the Peep is typically associated with approach behavior and may function to reduce aggression in conspecifics. She felt the Chuck ("Chee" call) served to attract attention, may give information about the presence of "non-specifics" in a squirrel's territory, and may serve to distinguish the sexes. Searing (1975, 1977) regards the Chee as an aggressive vocalization.

He had no playbacks of the Chee elicit alert responses (N = 14) while the Peep-Chuck sequence I used elicited an alert response in five of eight experiments. My data are in much closer aggreement with Smith's (1965) analysis of function of these vocalizations. He dealt with all the visual contact alarm calls described here as one catagory of alarm calls. He states, "The usual reaction of a red squirrel hearing an alarm call is to look in the direction of the caller. However, squirrels which are near the extremities of a tree branch will often react by running to the trunk and part way down the tree before looking." He indicated no difference in the situation in which alarm notes were used (i.e. no difference in response to avian versus ground predators). Smith states "The function of the call is to warn conspecific individuals of the presence of predators. The giving of the call seems basically altruistic because the caller is increasing its chances of being preyed upon by indicating its presence and position to the predator." The playback experiments done in this study indicate that the alarm calls are generally given after the subject squirrel had retreated to the safety of a tree where it had considerable protection from ground and avian predators. Sherman's study (1977) indicates alarm calling in Belding's ground squirrel can be explained by the social system. When alarm calls are given in a situation where closely related kin are the likely recipients, the caller can help its own inclusive fitness as described by Hamilton (1964) even if it should take the risk of becoming the predator's mark. The relatedness of individuals observed in this study was not known and whether or not

the red squirrels' social system would take advantage of nepotism in giving alarm calls has yet to be determined. Reciprocal altruism would be a more likely explanation for alarm vocalizations in the red squirrel since the extended family is not known to exist as it does in some ground squirrels suggested as using alarm vocalizations nepotistically (Sherman, 1977; Barash, 1975; Dunford, 1977). The fact that red squirrels maintain individual feeding territories would certainly make this an interesting sciurid to study in this regard to make comparisons with the more social ground squirrels.

There exists a diversity of alarm calls grading from mild alertness to high alarm excitement for the tree squirrels but all seem to be based on the "bark" note of short duration and very broad frequency range. The variations made on this theme both inter- and intra-specifically are numerous and are achieved with repetitions and additions.

The Scream, which was found in this study to serve as a "physical contact alarm" or distress vocalization, caused response in the playback subjects that was similar to responses to the visual contact alarm vocalizations except that there was a more pronounced movement into a tree followed by Peep vocalizations in response to the Scream. A squirrel that hears a Scream may be a more likely target of a predator since not only is a predator likely to be in the vicinity but it is probably in a feeding mood. The squirrels' general response of ascending a tree and freezing on the other side of the trunk will certainly aid their chances of avoiding detection by a predator. The Peep vocalizations following the playback

occurred mainly in one experiment and many more Peeps were given than in response to the Peep-Chuck or Trill PB experiments, possibly an indication of the greater intensity of alarm that the Scream elicits over the visual contact alarm.

Smith (1965) deals with the function of vocalizations in Tamiasciurus hudsonicus and T. douglasii as essentially the same in both species except for some differences in physical structure of notes. Though he didn't record the vocalization, Smith indicates that the Scream "could serve to startle or confuse the attacker and thus aid the squirrels' escape." Even if this does serve as a viable function of the Scream, this study shows that other squirrels may make use of the information they get from this call. The Scream has been reported in the literature by Klugh (1927, p. 31) where he states, "The note of pain is a rather shrill scream. I have heard it from an intruding squirrel when bitten by the owner of the stores it was raiding." Dice (1921, p. 6) reports "screaming" from a young squirrel when it fought while being attacked by a mink. Shrill cries, squeals, or screams are described for Sciurus carolinensis (Horwich, 1972), S. niger (Zelley, 1971), and S. aberti (Farentinos, 1974) as being distress type calls, particularly of nestling or young squirrels, during adverse physical contact such as during handling or when being carried away by a predator. Embry (1970) does not discuss a Scream, a distress call, or a note of pain in her paper.

Strong territorial behavior is found in the genus Tamiasciurus and here we also find a vocalization strongly associated with

territorial announcement. The Chatter vocalization is relatively loud (The Chuck and Trill are the only vocalizations with higher average peak db levels. See Table 2.) and has a physical structure which makes it easily localizable (i.e. broad frequency range covered, sharp onset and offset of the notes, and relatively long duration of each vocalization) (Marler, 1966). Fifty percent of the Chatters heard in the field (See Table 9.) were given when no other squirrels were known to be in the area and when Chatters were directed at the observer or another squirrel, they were possibly stimulated by the invasion of their territory. The fact that the Chatter is given in a variety of situations causes the argument that this vocalization may function as territorial announcement ("advertisement", Embry, 1970) or aggression (Searing, 1975). The evidence reported in this paper strongly supports the major function of the Chatter as being territorial announcement but cannot refute the possibility of other functions in some contexts.

The Chatters given by males during mating chases (which generally do not occur on their feeding territories) can be considered as "territorial" announcement with the estrous female serving as property. This agrees with Smith's (1965) statement that, "The territorial call appears to serve the dual function of advertising ownership of an area and of intimidating other squirrels who might contest ownership. The same call is used whether the area is defended in order to protect a food supply or in order to protect a female in heat. The giving of territorial calls by females in heat has no obvious function as nothing is defended and may

constitute a territorial drive that is not suppressed during breeding activity." The Chatter's function "of intimidating other squirrels" is stressed by Searing (1977) as being solely aggressive in nature.

The occurrence of one or more Chatters following more than one third of the releases (Table 14) is a further indication of the need of the captured squirrel to reaffirm its ownership of an area after having been away from it for some time.

The morning chorus (Fig. 14) of Chatter vocalizations is closely associated with the general activity level of the squirrels in the early morning. Since the squirrels are more active, encounters which elicit the Chatter are more likely to occur. The morning chorus includes spontaneous chatters by the squirrels, possibly serving to establish at the outset of their activity which areas are occupied and defended.

Figs. 10 and 13 indicate very little significant response by the squirrels to playbacks of the Chatter vocalization. It is at first thought surprising that a Chatter given in close proximity to a red squirrel should not produce more of a response than was observed. However, the fact that there is significantly increased orientation toward the speaker following the playback may indicate that visual contact with an intruder may be necessary before the other behavioral aspects measured would come into play in the subject's response to a Chatter. This may be an adaptive response to save energy in responding to a vocalization which occurs commonly and does not always indicate a threat to the squirrel hearing it.

Only if an intruder is an immediate threat to another's territory, will defensive actions be taken by the territory holder.

Searing (1975) found that red squirrels respond to "chir" calls of other squirrels within approximately a 140 meter radius. Models in aggressive and eliciting postures were generally found to produce no response from another squirrel in his study, whether still or moving, used alone or accompanied by a vocalization. Searing did observe displacement grooming following playbacks without a model so the subject squirrels' behavior towards the models may indicate they offered no threat. He also noted that the PB of a "chir" frequently elicited chir calls when played more than 30 m from a midden. This study found Chatters made by the subject squirrel (within 30 m of the speaker) in three of six experiments and Chatters by other squirrels following the playback (from 10 m, 30 m, 30+ m, and 2 unknown distances) in five of those six experiments.

Searing's methods are somewhat vague, the sound level and length of the "Chirs" played back are not reported and there is no indication of controls against habituation. In fact, the results of his individual call recognition experiments suggest that habituation did occur when using that particular experimental design. The sampling methods used in collecting his data for the number of "chirs" per hour are also absent from his paper.

Vocalizations associated with intraspecific aggressive behavior are known for the gray (Horwich, 1972) and Abert's squirrels (Farentinos, 1974) and probably exist for the fox squirrel as well

(Zelley, 1971). In the red squirrel such vocalizations of aggressiveness include the Whine, Multiple-Chucks, Growl, and Chuckle. Smith (1968) calls the Whine the "loud aggressive call" and the Growl the "soft aggressive call." The data presented in Table 2 indicate that the opposite may be true for the population studied in this paper where the average peak db level of the "loud aggressive call" is 66.9 and the "soft aggressive call" is 68.6. Whines occurred with a Chatter in nearly 70% of the observations presented in Table 10. When such Chatter-Whine combinations were observed as being directed at a specific squirrel, the target squirrel, if not in a trap, was always displaced (See Table 9B.). In the twenty cases where a Whine was given without a Chatter, nine of the target squirrels were displaced (See Table 10.).

The playbacks using the Whine vocalization caused significant changes in the subjects' alertness, orientation, and vocal behavior. The played back Whines may have indicated an immediate threat to them, thereby stimulating a high level of responsiveness. The increase in Peep vocalizations following playback may be a further indication of the subjects' alertness to the situation. Embry (1970) states that Whines "serve as an aggressive sound of active defense. If this is the case, the rolled R call (Chatter) would be heard more frequently, even in the absence of other squirrels. Squeaks (Whines) would only occur under the less frequent situation of immediate threat to a territory and/or the approach of a conspecific or his vocalizing nearby." Smith (1965) says that the Whine is used only when the caller actually saw another squirrel that was an

immediate threat to its territory. He also notes that it was given at least once during breeding activity, so it is used in defense of more than just a food supply.

Smith states that the Growl is probably used when the intended hearer is within about ten feet of the caller whereas the Whine is used when the intended receiver is at a greater distance. This distance relationship was also observed in this study with the additional aspect of the Multiple-Chucks acting as an aggressive call towards conspecifics at intermediate distances. (Exact numerical distances cannot be given since there is much overlap in the distances at which Growls, Whines, and Multiple-Chucks are given.) Embry (1970) called these Multiple-Chuck vocalizations "Trills" and dealt with them in her analysis of "Chee" calls and made no indication of difference in function. This study indicates a definite aggressive function in the Multiple-Chuck with fifty percent of the target squirrels being displaced.

The Growl vocalization was observed to be given in response to other squirrels during chase encounters and has a wide range of sound levels (See Table 2.). These sound levels indicate a graded response by the vocalizing squirrel to the intensity of the encounter. A mild encounter may elicit a few soft Chuckle notes whereas an intense encounter involving physical contact will elicit louder and longer Growl vocalizations. The function of the Growl vocalization given by Embry (1970) and Smith (1965) are in agreement with the findings of this paper.

The Buzz vocalizations observed in this study were used in

situations that support Smith's (1965) attributed function of appeasement. This is not in agreement with Embry (1970) who states that this vocalization is more commonly used in parent-young and sibling relationships, denoting comfort rather than needs. It is important to point out the fact that all of Embry's observations of this vocalization were on juveniles whereas Smith observed it largely in adults. Farentinos (1974) describes a similar situation in the Tassel-eared squirrel (S. aberti) where a vocalization used by juveniles reappears in adult males who direct it at an estrous female while trying to approach her in a mating chase. The stifled-sneeze (Bakken, 1959) of S. carolinensis appears to have the same function as this adult squeal described by Farentinos and the Buzz vocalization in Tamiasciurus hudsonicus. These spectrally different calls are given by males of the species when following estrous females, and also (in S. aberti and T. hudsonicus) by subordinates while being chased. The buzzing type sound of T. hudsonicus is spectrally nearly identical to the buzzing in S. carolinensis as reported by Horwich (1972). The buzzing in the gray squirrel, however, is attributed with the function of indicating mild alarm.

To my knowledge the high-pitched Squeak vocalization has not been previously reported in the literature and was observed only once in this study in a laboratory situation in mid-February of 1975. The female squirrel vocalized these very weak sounding vocalizations while being handled and may be another type of distress vocalization but not likely for long distance communication. Though I have little information in regard to this vocalization, I have included it here

for completeness.

The tail movements described herein as being a component of the non-vocal acoustic communication of red squirrels are probably mainly incorporated for the visual signal component. The situations in which the tail does produce sound on the substrate, however, will add to the attention-getting value of the tail movement.

Tooth chattering has been recorded by Zelley (1971) for the fox squirrel, Horwich (1972) for gray squirrels, and here for red squirrels, and it's likely it occurs in all the tree squirrels. The chattering itself is not loud so must serve solely as a close range signal unless the visual component is involved. It occurs in gray squirrels preceding or following aggressive encounters, and after a long chase may be accompanied by growling and rapid tail waving. Zelley (1971) simply states that it occurs in fox squirrels during situations of mild unrest. I have observed it in gray squirrels in mild disputes over food and have recorded its occurrence in captive red squirrels in response to close observation.

Drumming, foot stomping (Bakken, 1959), or forefoot thumping (Farentinos, 1974) is reported by Horwich (1972) to be a response to general excitement or alarm and has been seen by him in captive flying squirrels (Glaucomys volans), red squirrels (T. hudsonicus), and in fox squirrels (S. niger) as well as in gray squirrels (S. carolinensis). He describes this behavior as the alternate and rhythmical movement of the squirrel's feet up and down in place and notes that the temporal rhythm is faster, the smaller the squirrel species. The spectrogram of drumming included in this paper will

allow quantitative measures of this behavior to be compared between species in the future. Though the drumming descriptions for S. aberti and S. carolinensis indicate the forefeet as being moved, my observations of the red squirrel find drumming occuring from the hind feet and only rarely from the forefeet. Sumner and Dixon (1953) report that it was the forefeet of the Western Gray Squirrel (Sciurus griseus) that were stamped in response to a blue-fronted jay that alighted on the bird feeding platform the squirrel had commandeered. Drumming does have acoustic properties but does not always occur on a surface conducive to producing sound.

Farentinos (1974) notes a sound similar to drumming but much louder "was produced when a squirrel ran rapidly up or down the trunk of a tree as occurred during chases between individuals or while escaping from a predator. I could easily hear this sound at a distance of nearly 100 m." Zelley (1971) notes that a particular vocalization ("Chatter barks") is given by the fox squirrel while it is running along a tree limb or trunk, or while rapidly climbing a trunk escaping from an observer. A rapid ascent sound occurs in the red squirrel accompanied by a similar trill type vocalization. This rapid ascent connotates an acoustic signal distinct from squirrels chasing on a trunk in that it is one squirrel making one (or several, but separated) short duration sounds rather than two or more squirrels making a rather continuous sound or at least much longer in duration than a rapid ascent type sound. Certainly the noise of a chase will transmit information to other squirrels but the context, and meaning of the noises are different and the two

should be dealt with accordingly.

Although the red squirrel produces acoustical sounds that serve the functions of alarm, aggression, appeasement, and territorial announcement, it should be emphasized that a given call type can be used for different functions depending on the context of the situation. It is possible to assign a particular function to a given vocalization when that is its main use, but we should be ware of labelling a vocalization with an exclusive function.

Gradation of intensity of vocal displays in Tamiasciurus hudsonicus with increased volume and repetition rate as well as addition of other components, both visual and vocal, make for a richness in the character of this loquacious creature but at the same time serve valuable functions of protecting a territory, acquiring a mate, or indicating the intensity of alarm. The red squirrel does have something to say if we will only stop to listen.

SUMMARY

This study describes the vocalizations used by the red squirrel (Tamiasciurus hudsonicus) collected over an eighteen month period at Itasca Biological Station, Minnesota. Sound levels of several of the vocalization types were measured and playback experiments were conducted in the field. Results of the playback experiments and field observations of acoustic behavior were analyzed to determine the function of the various vocalizations.

Individual vocal types were found to be used for different functions depending upon the contextual setting. Gradations between different vocal types were found and presented. Vocalizations were functionally classified into the following catagories: visual contact alarm, physical contact alarm (distress), territorial announcement, aggressive intent, and appeasement.

Implications of this study in regard to the red squirrels' social system are discussed and comparisons are made with the published literature on vocal communication of North American tree squirrels.

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APPENDIX A:

FIGURES

Figure 1. Grid map of Itasca Biology Station study area.

University of Minnesota

FORESTRY AND BIOLOGICAL STATION

Grid Map

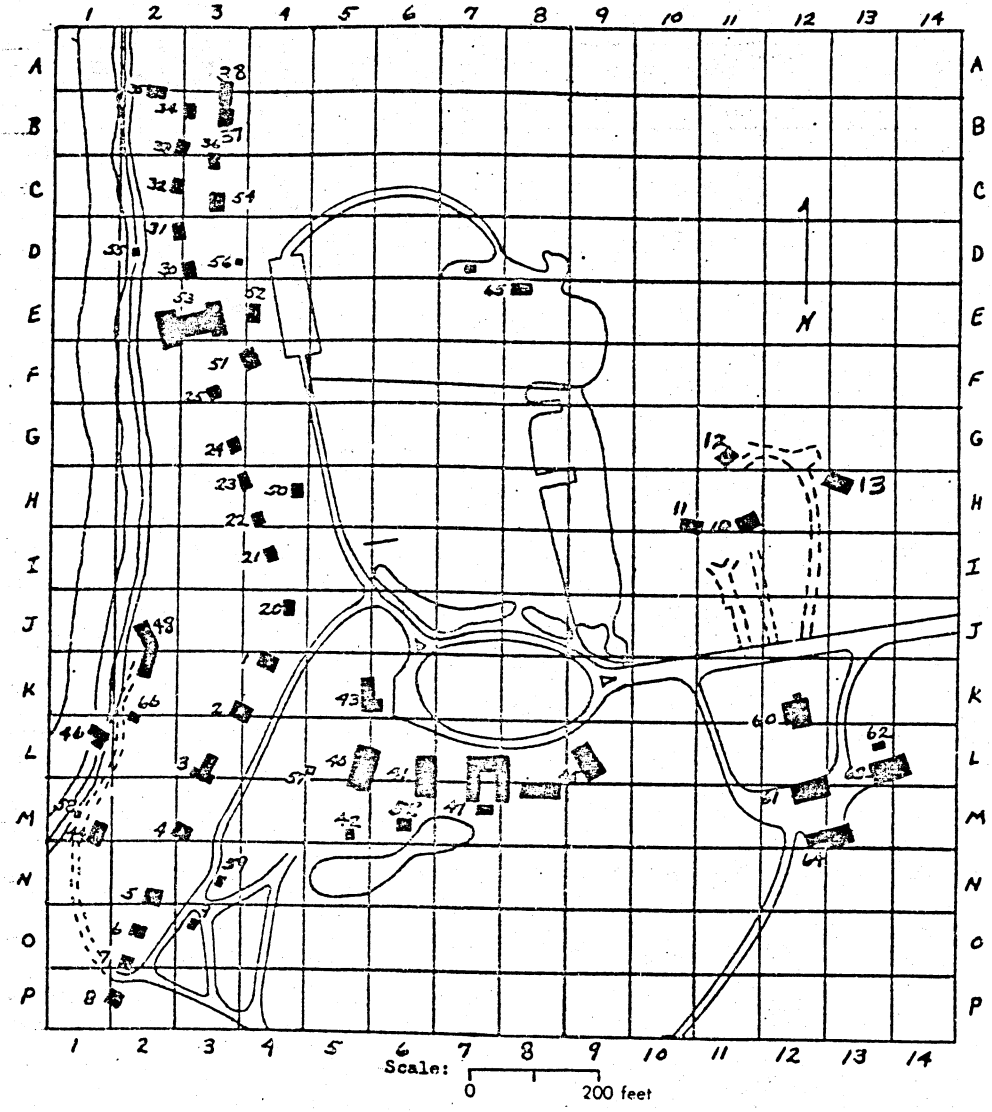

Figure 2. Dye-marking number locations. Use of adjacent positions was avoided to aid field identification. Both legs were marked for "seven" and "eight" so that identification could be made from either side of the squirrel.

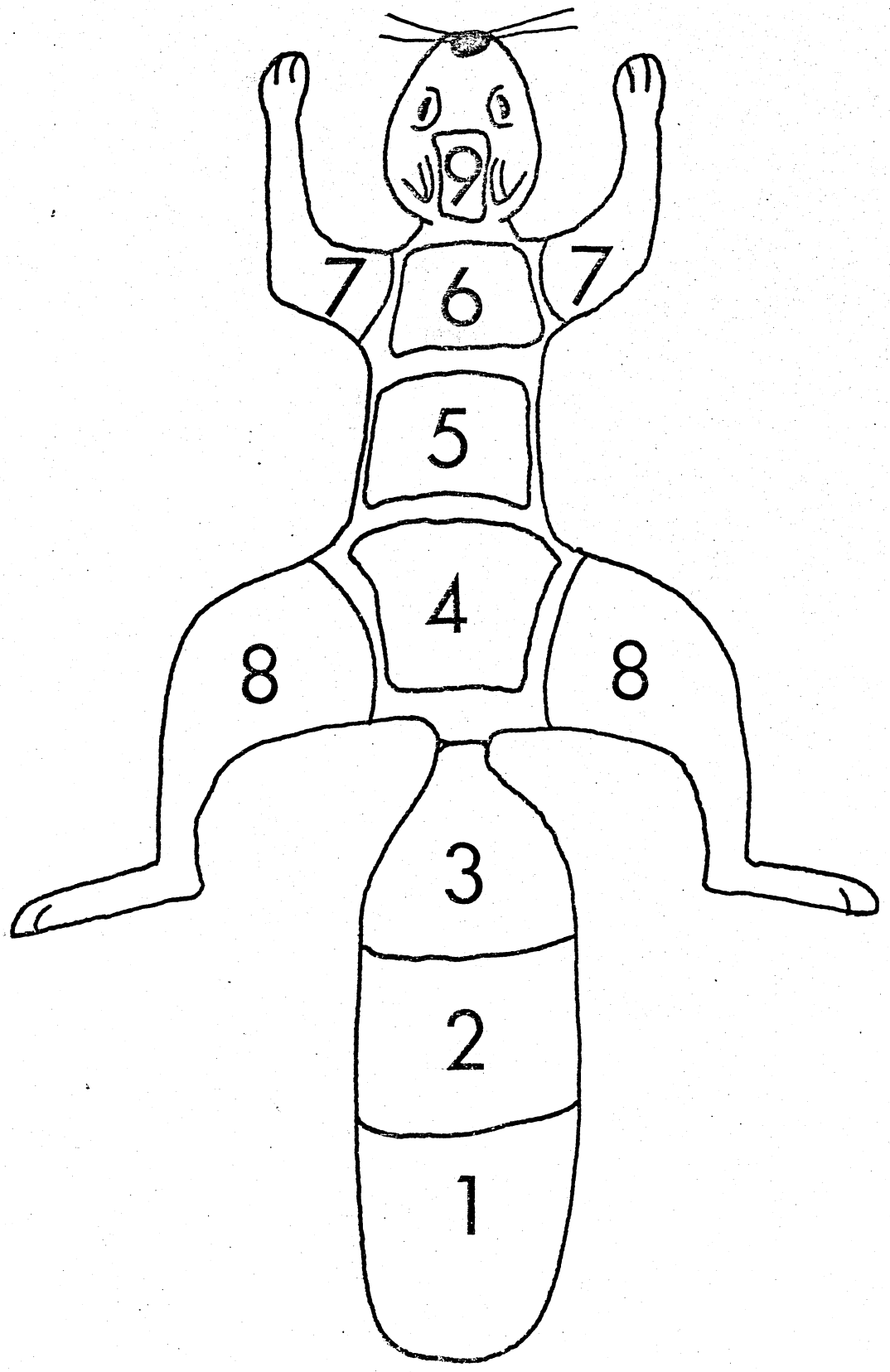
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Figure 3. Sonograms of red squirrel vocalizations: a) fourteen Peeps and three Groans; b) an alpha-beta Chuck, five beta-Chucks, two three harmonic Peeps, each followed by a beta-Chuck, and an alpha-beta Chuck with a three harmonic alpha component; c) a single three harmonic Peep followed by a Trill; d) a two harmonic Peep, single harmonic Peep, faint two harmonic Peep, and a Trill followed by a sound made by the squirrel's claws on the bark but accompanied by only a single, very faint Peep; e) a Trill preceded and followed by Peeps; f) a Scream vocalization; g) a complete Chatter vocalization. Note the change in repetition rate towards the end of the vocalization. This is the Chatter used in the playback experiments; h) a series of nine Whine notes.

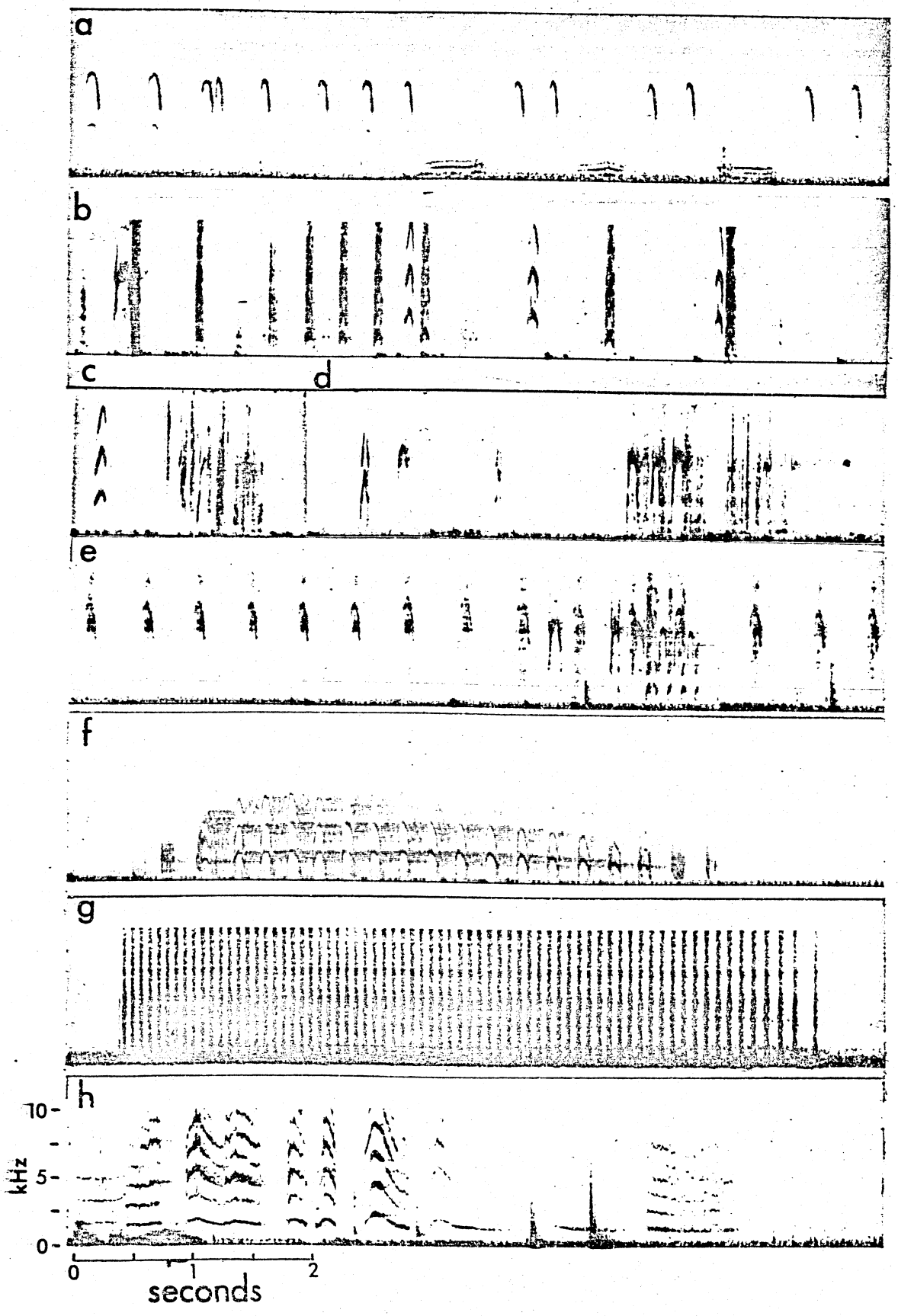
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Figure 4. Sonograms of red squirrel vocalizations: a) a series of three Multiple-Chucks composed of two, three, and four alpha-beta Chucks; b) another series of Multiple-Chucks (rerecorded from a cassette note tape); c) a series of eleven Growl vocalizations; d) eleven Squeak vocalizations. Sound at 5 kHz and below is an artifact of laboratory noise; f) two short bouts of drumming (hind feet); g) a portion of the Chickadee vocalizations used for the control playback experiments.

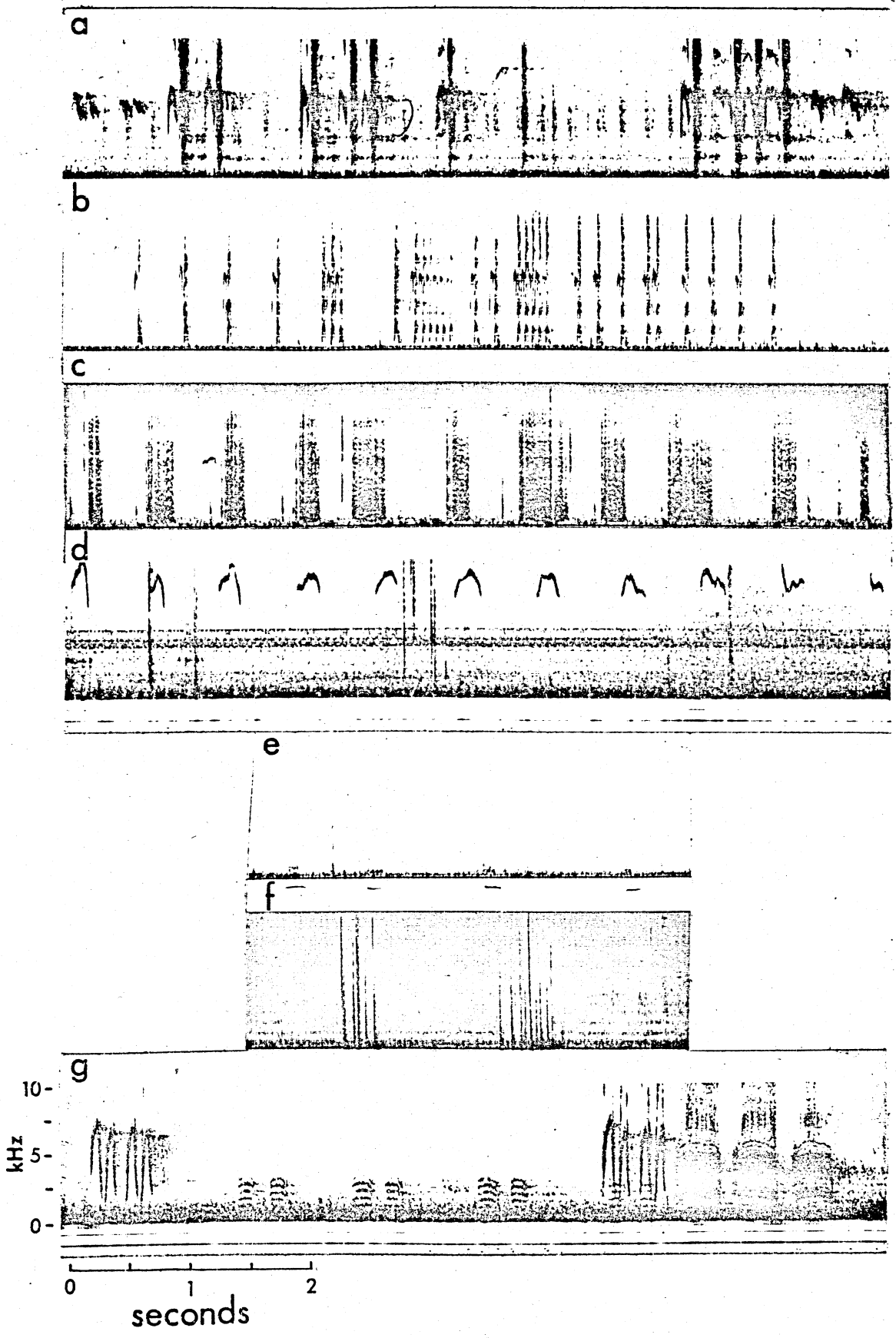
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Figure 5. Gradations of some red squirrel vocalizations: a) a series of Whines grading into a series of Growls; b) variation in length and tonal quality of Whines (this sequence used for the playback experiments using Whines); c) indication of the variability in Peeps caused by changes in the internote interval; d) gradation between beta-Chucks and Growl; e) Growl grading into Groan.

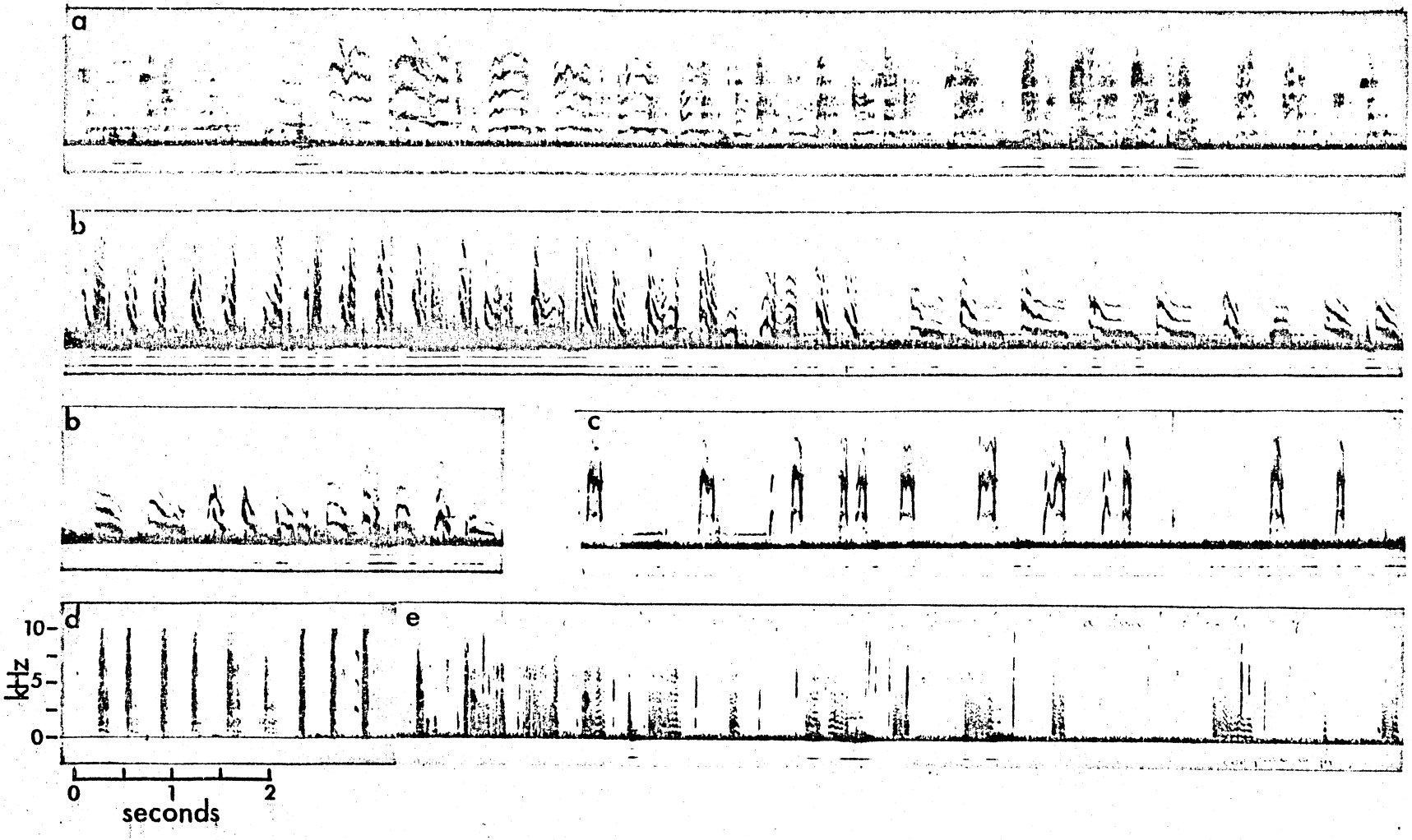
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Figure 6. Gradations of some red squirrel vocalizations: a) short Growl notes repeated rapidly grading into a Chatter; b)Growl grading into a Scream; c) gradation of Scream notes to Growl notes and vice versa; d,e,f) Growls grading into Chuckles. The broad frequency band noise which occurs in f is from blowing which ellicited the Chuckle notes; g,h,i) Peep vocalizations accompanied by scratching of the tree bark.

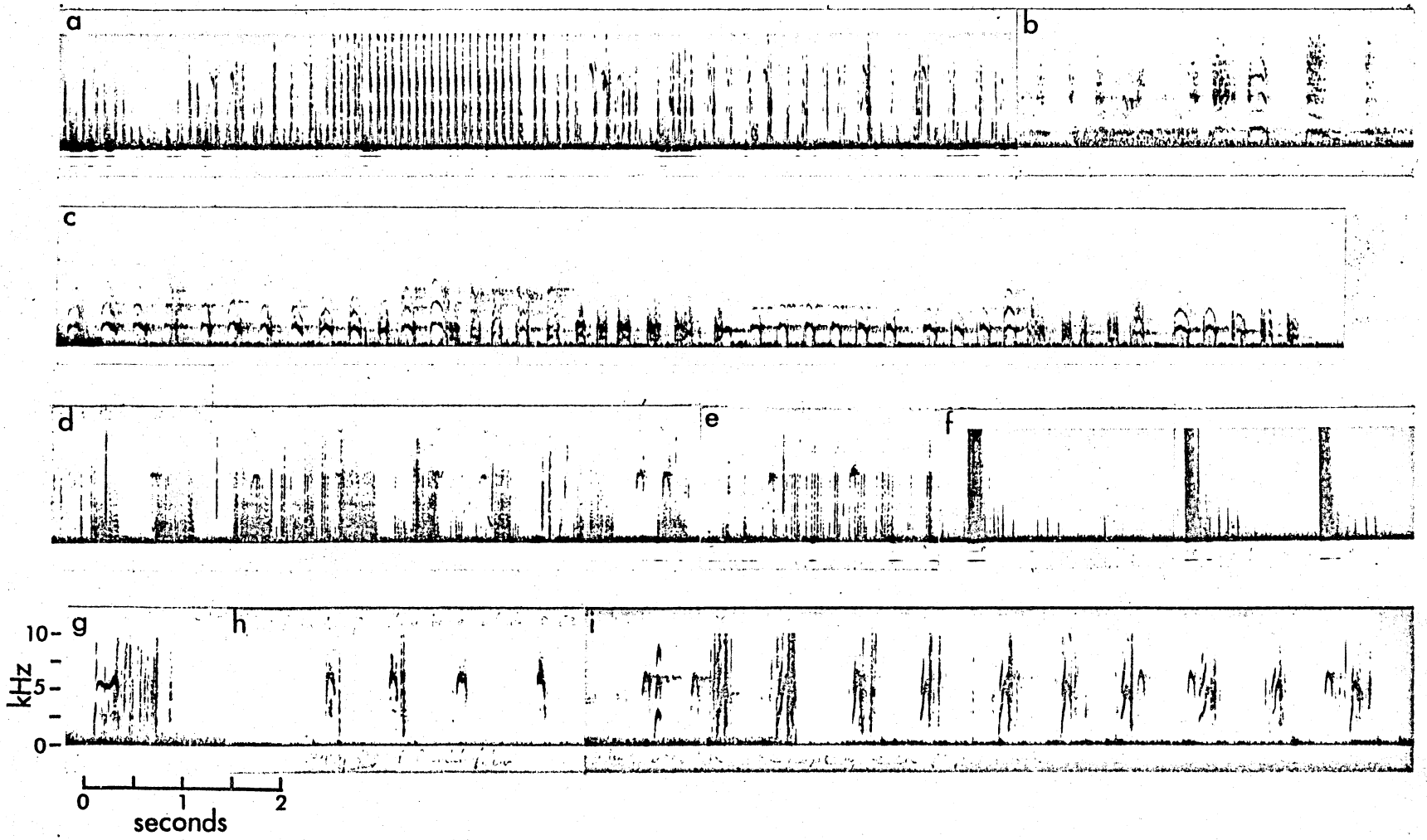
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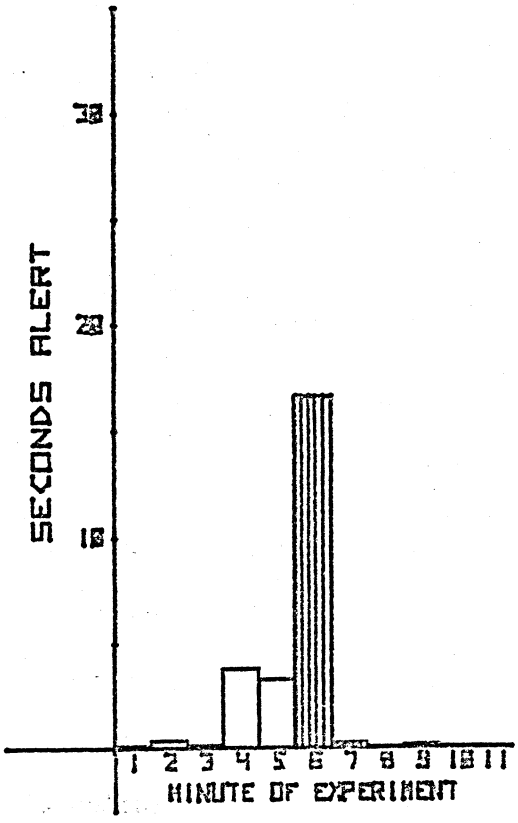
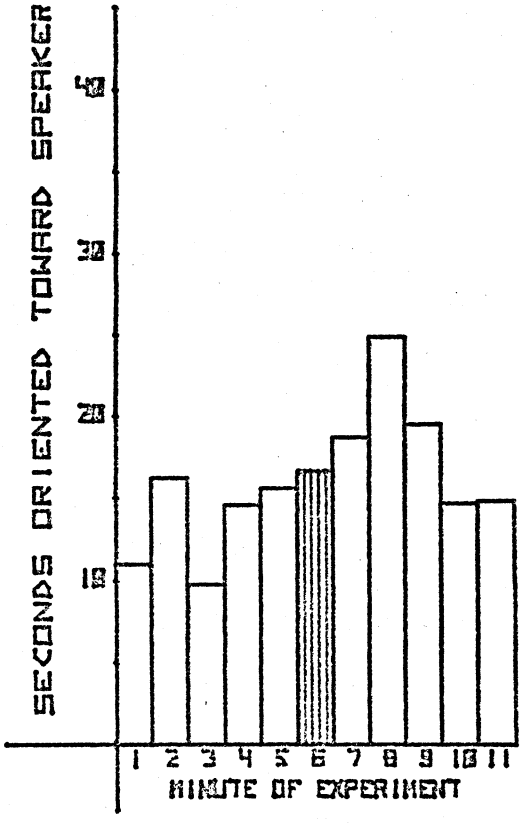
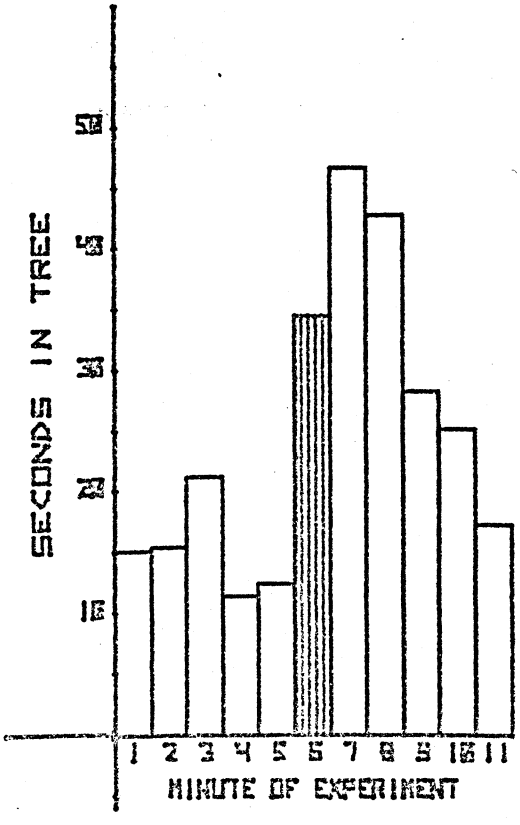
Figure 7. Histograms of behavioral responses of the red squirrel to playbacks of a one minute alarm sequence of 127 Peep, twelve Chuck, and three Groan vocalizations. Minutes one through five constitute pre-playback observations and minutes seven through eleven are post-playback observations. The striped line indicates behavior observed during the minute of playback. All temporal measurements were made to the nearest second and all histogram entries are the average per minute per squirrel. N = 8 experiments on eight different squirrels.

Red Squirrel Response to Playbacks of Peep-Chuck Vocalizations







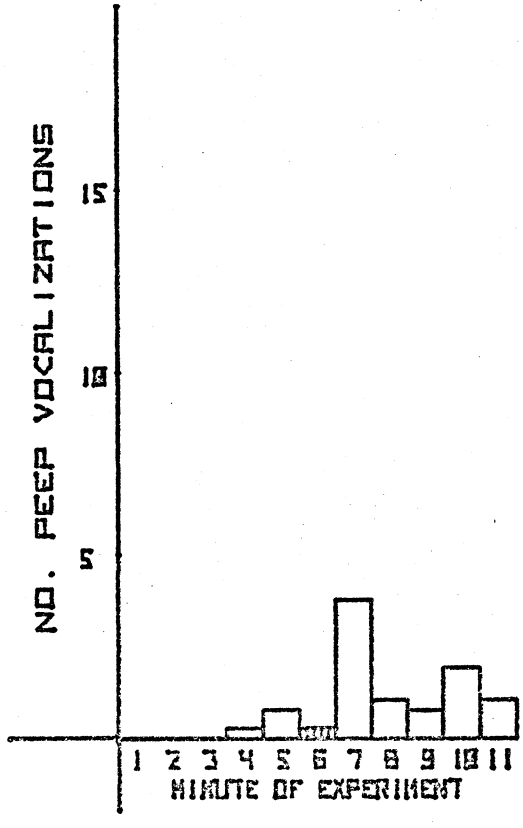
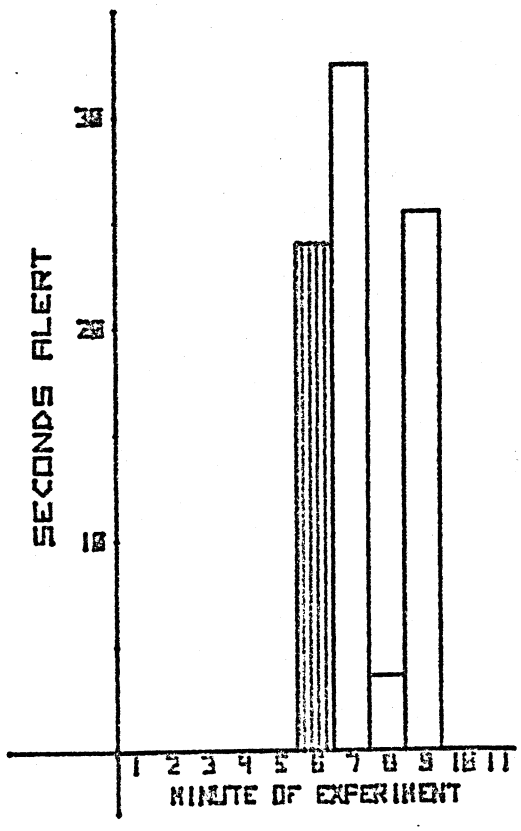
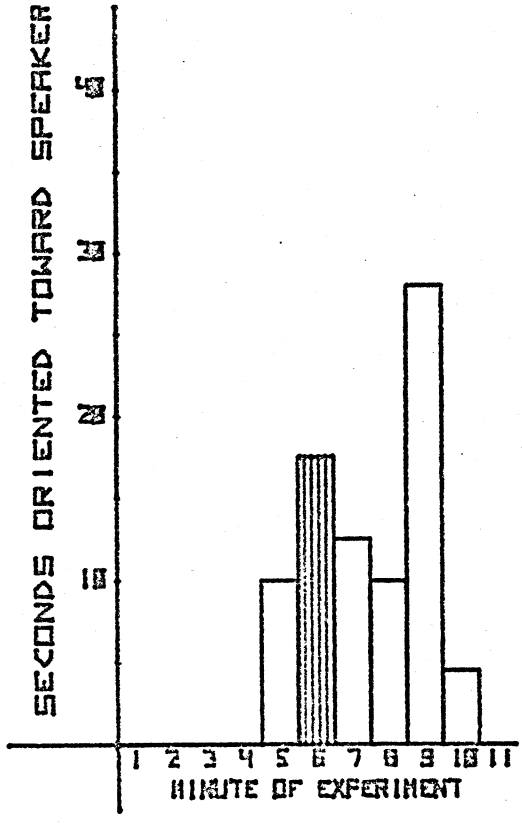
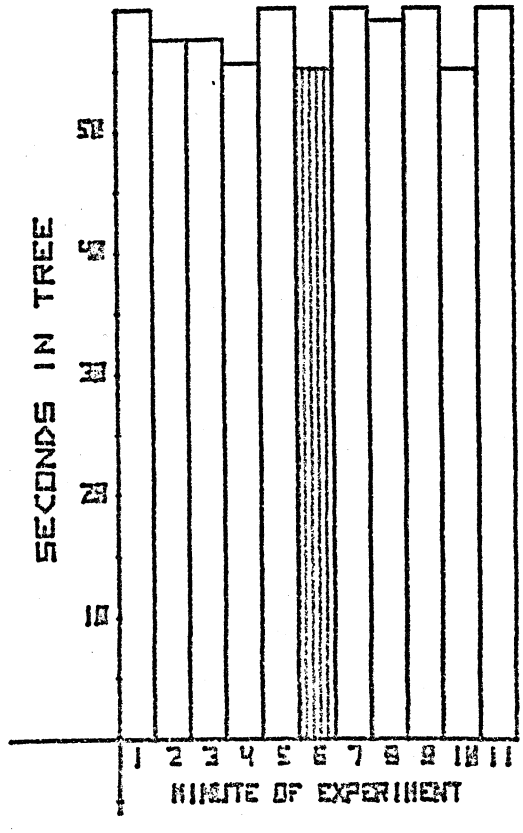


Figure 8. Histograms of behavioral responses of the red squirrel to playbacks of a Trill vocalization (preceded by five Peeps) three times during one minute. Minutes one through five constitute pre-playback observations and minutes seven through eleven are post-playback observations. The striped line indicates behavior observed during the minute of playback. All temporal measurements were made to the nearest second and all histogram entries are the average per minute per squirrel. N = 2 experiments on two different squirrels.

Red Squirrel Response to Playbacks of Trill Vocalizations







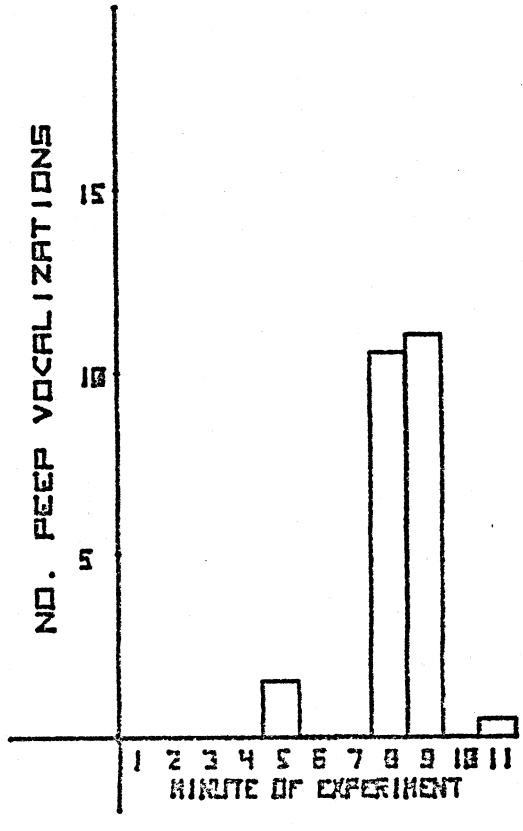
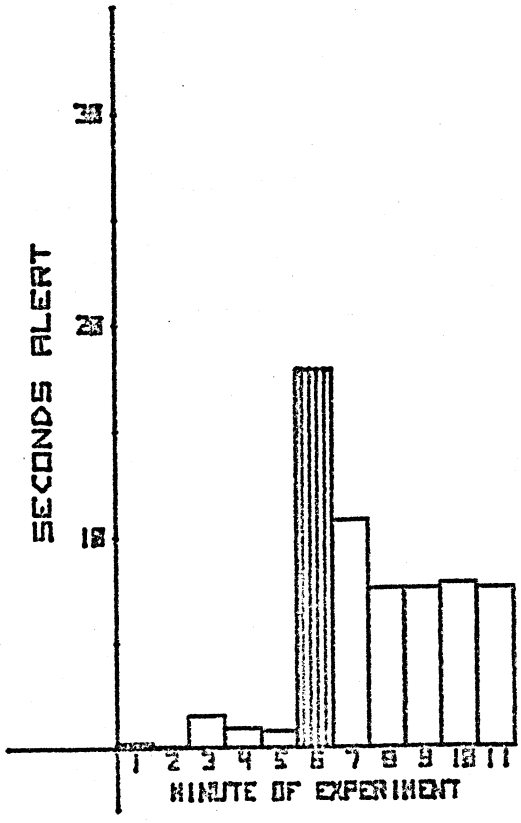
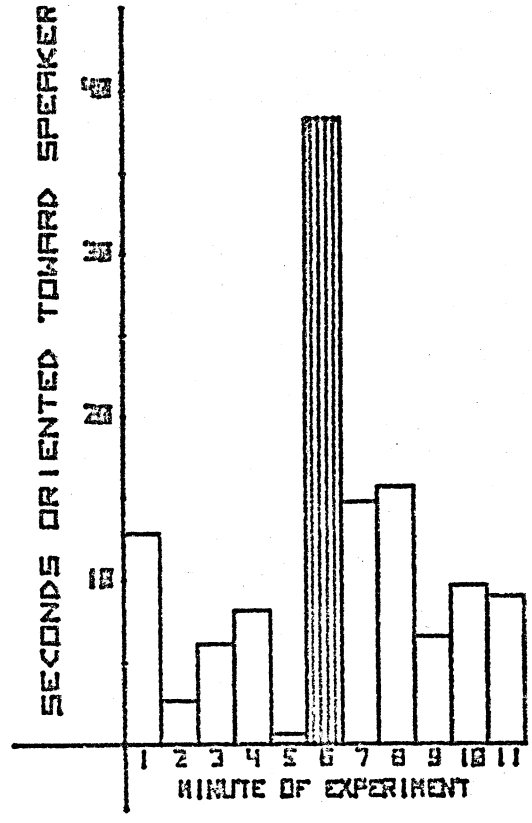
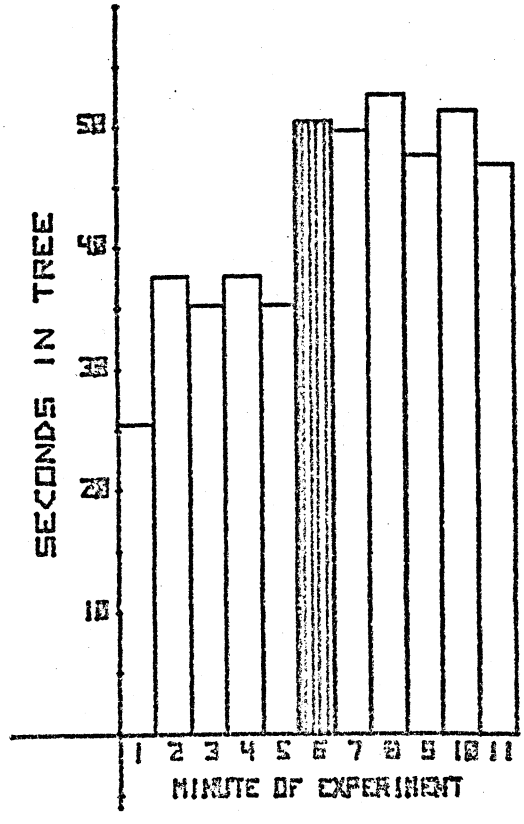


Figure 9. Histograms of behavioral responses of the red squirrel to playbacks of a series of Whine vocalizations three times during one minute. Minutes one through five constitute pre-playback observations and minutes seven through eleven are post-playback observations. The striped line indicates behavior observed during the minute of playback. All temporal measurements were made to the nearest second and all histogram entries are the average per minute per squirrel. N = 8 experiments on eight different squirrels.

Red Squirrel Response to Playbacks of Whine Vocalizations







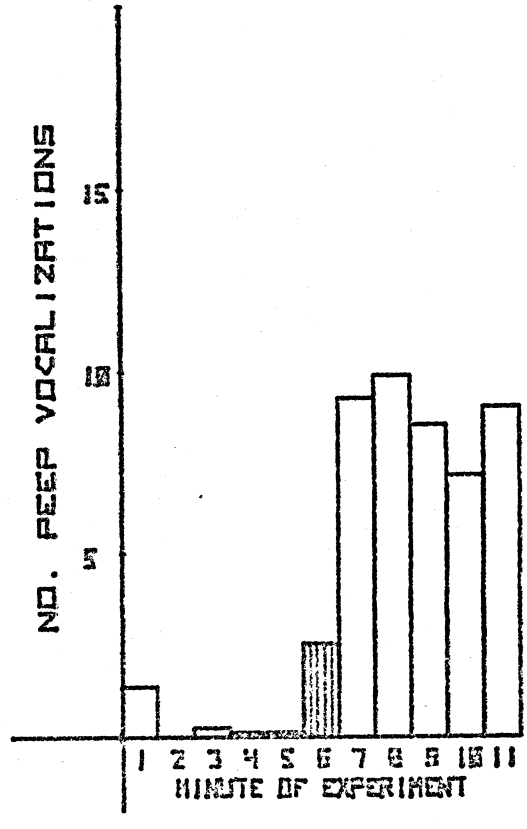
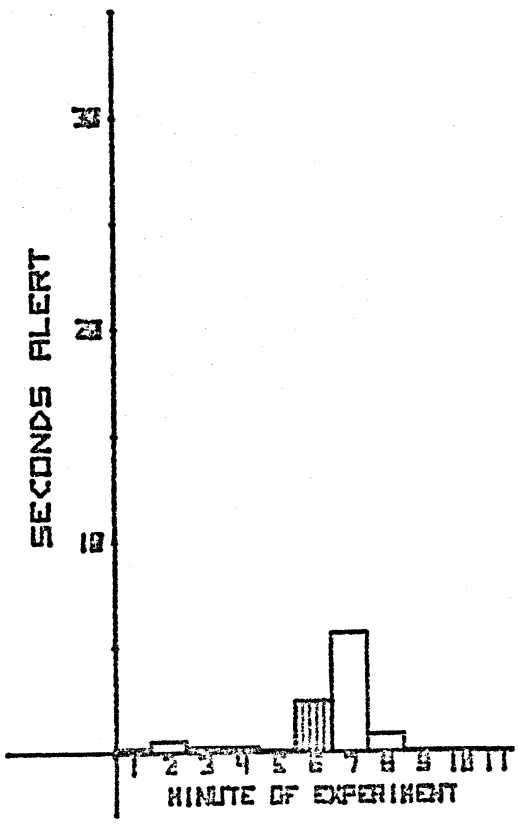
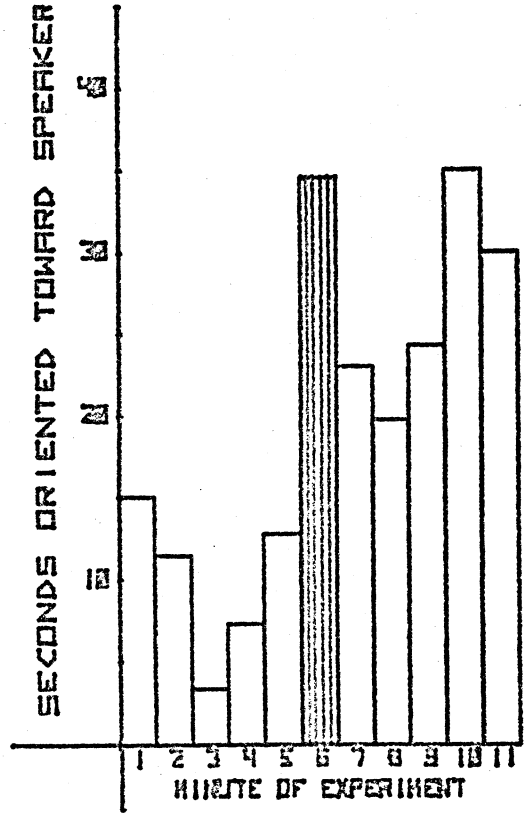
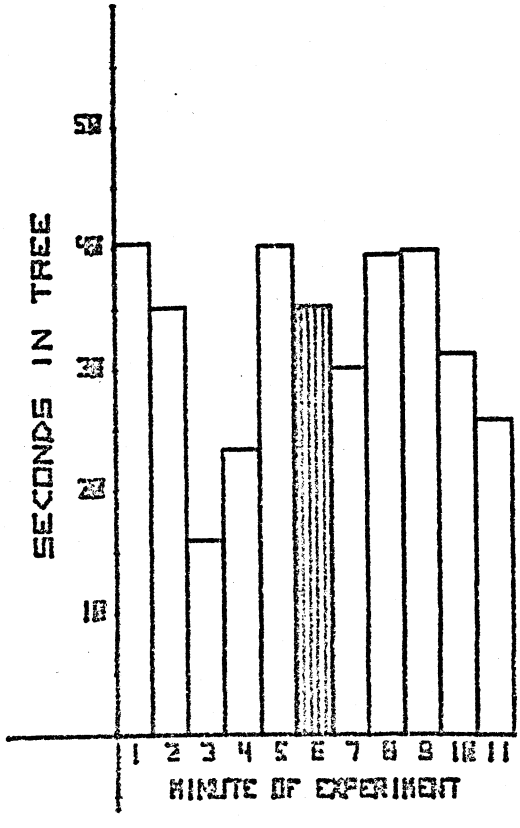


Figure 10. Histograms of behavioral responses of the red squirrel to playbacks of a Chatter vocalization three times during one minute. Minutes one through five constitute pre-playback observations and minutes seven through eleven are post-playback observations. The striped line indicates behavior observed during the minute of playback. All temporal measurements were made to the nearest second and all histogram entries are the average per minute per squirrel. N = 6 experiments on six different squirrels.

Red Squirrel Response to Playbacks of Chatter Vocalizations







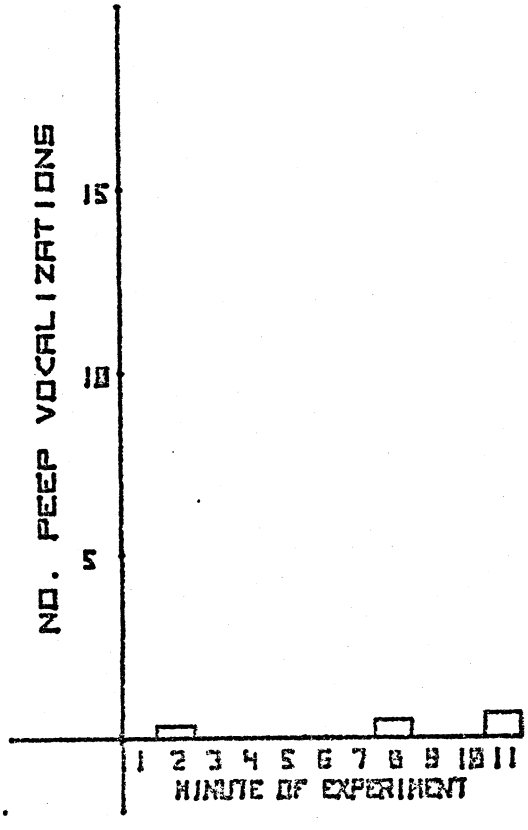
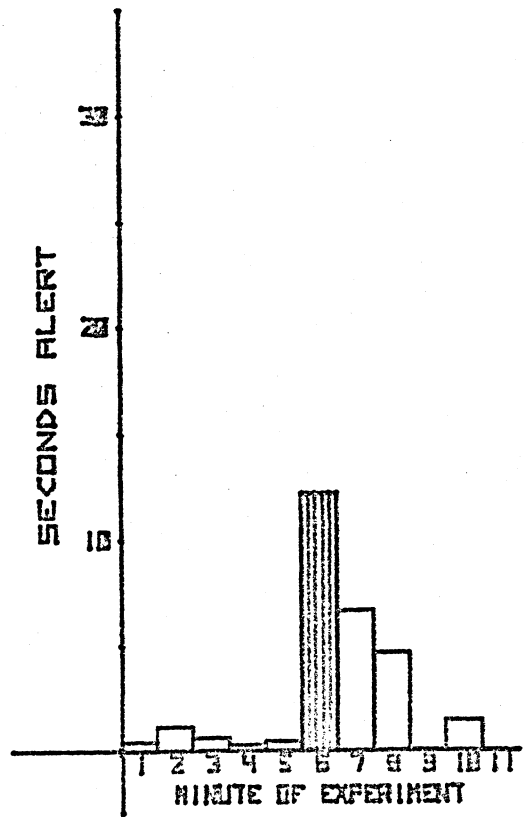
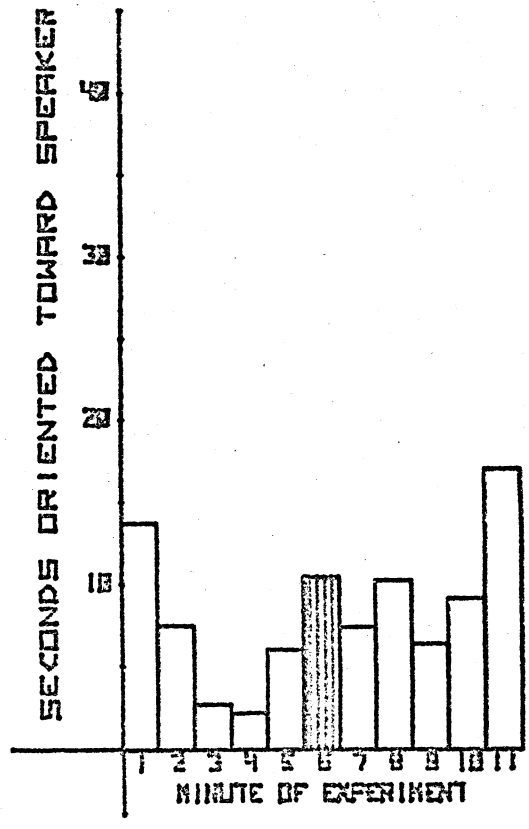
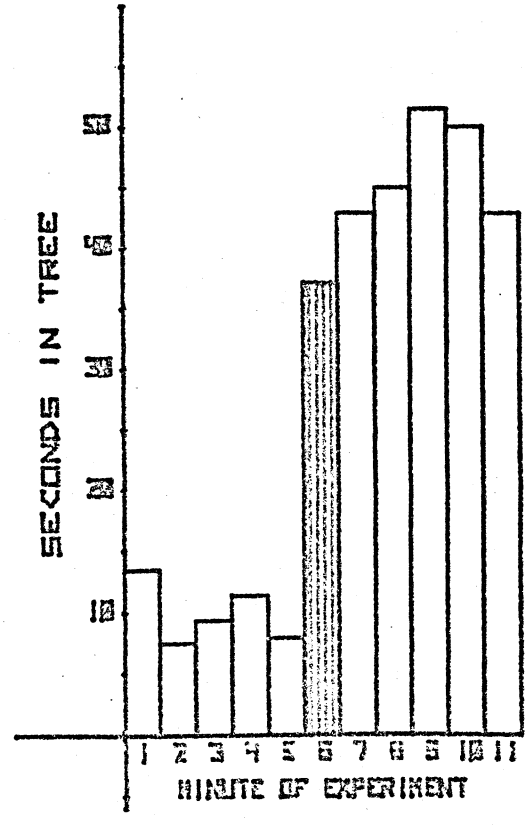


Figure 11. Histograms of behavioral responses of the red squirrel to playbacks of a Scream vocalization three times during one minute. Minutes one through five constitute pre-playback observations and minutes seven through eleven are post-playback observations. The striped line indicates behavior observed during the minute of playback. All temporal measurements were made to the nearest second and all histogram entries are the average per minute per squirrel. N = 7 experiments on seven different squirrels.

Red Squirrel Response to Playbacks of Scream Vocalizations







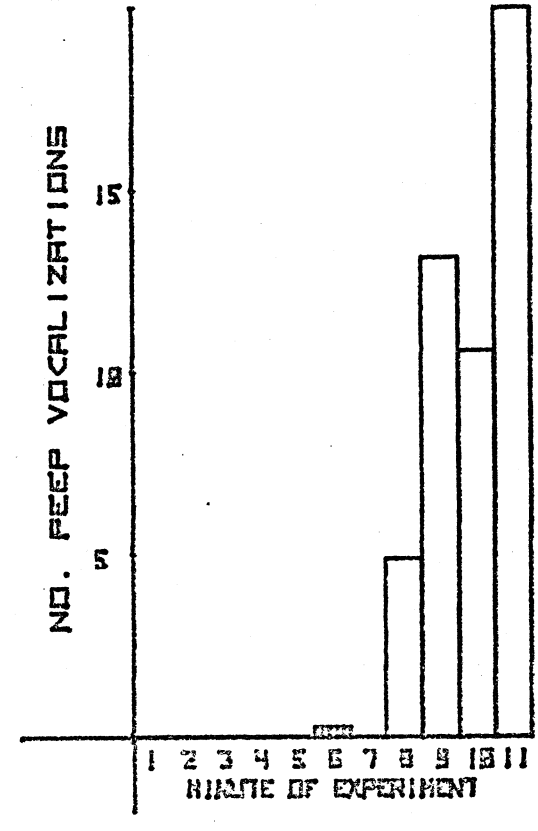
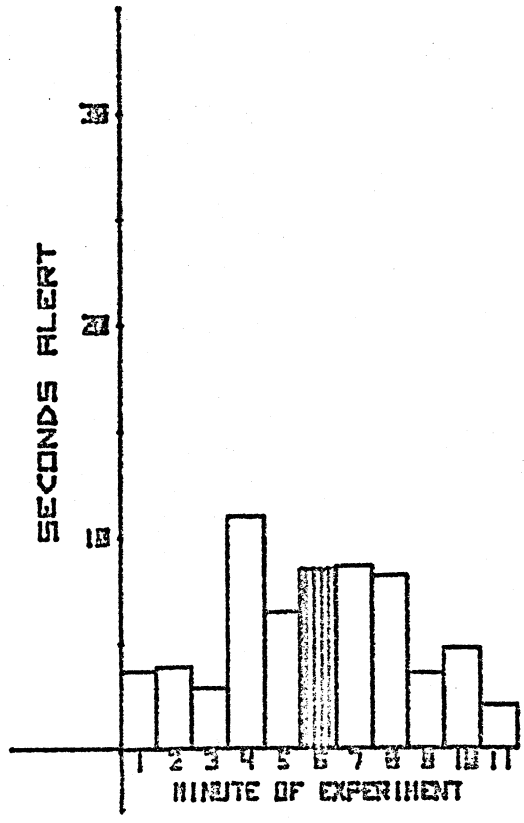
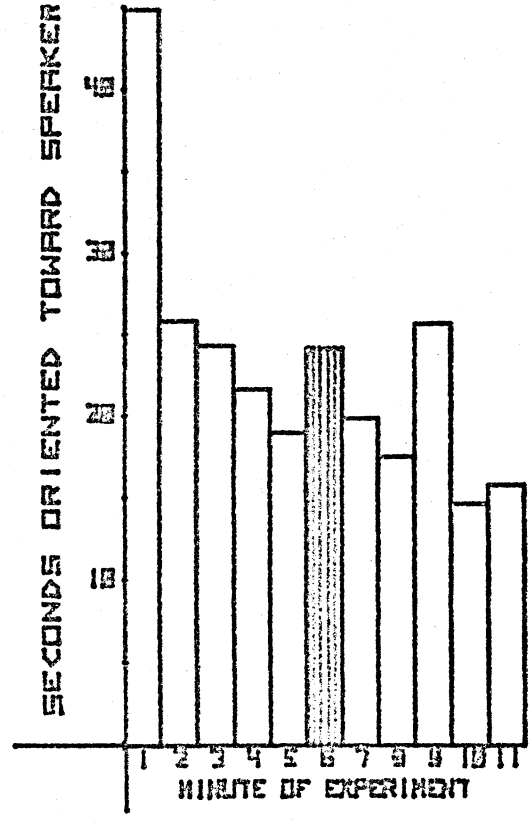
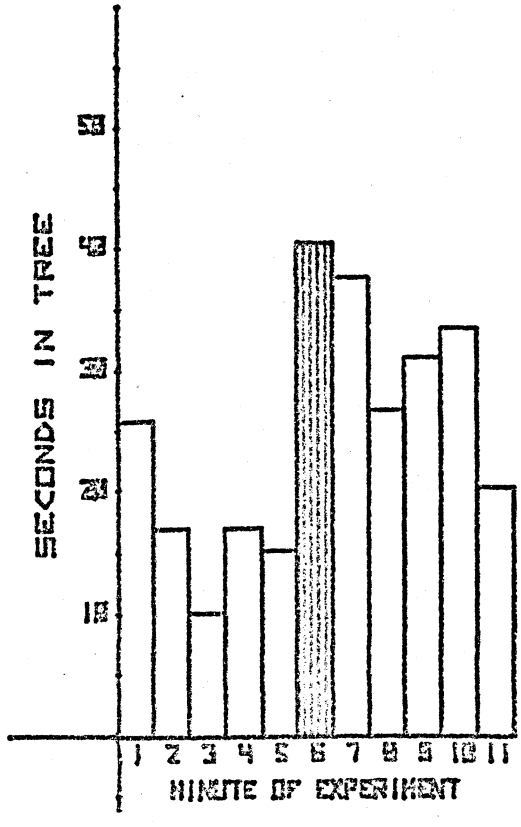


Figure 12. Histograms of behavioral responses of the red squirrel to playbacks of a one minute sequence of Chickadee vocalizations. Minutes one through five constitute pre-playback observations and minutes seven through eleven are post-playback observations. The striped line indicates behavior observed during the minute of playback. All temporal measurements were made to the nearest second and all histogram entries are the average per minute per squirrel. N = 7 experiments on seven different squirrels.

Red Squirrel Response to Playback of Chickadee Vocalizations







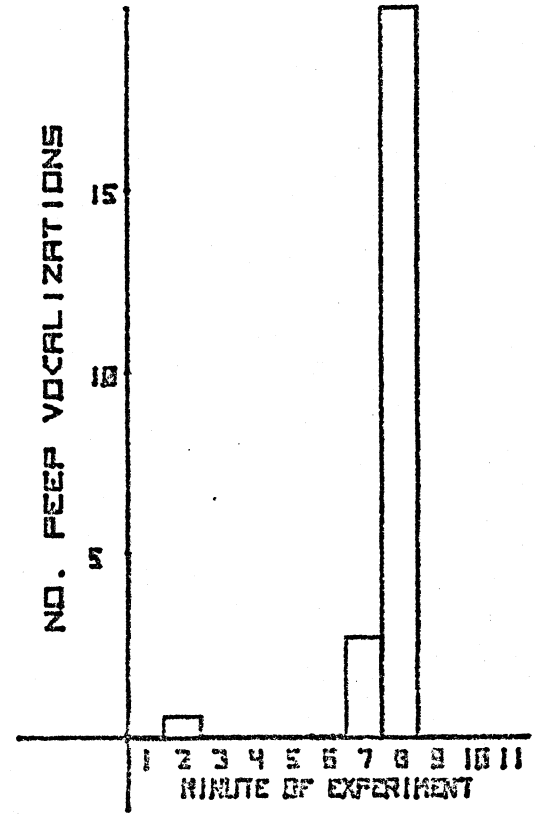
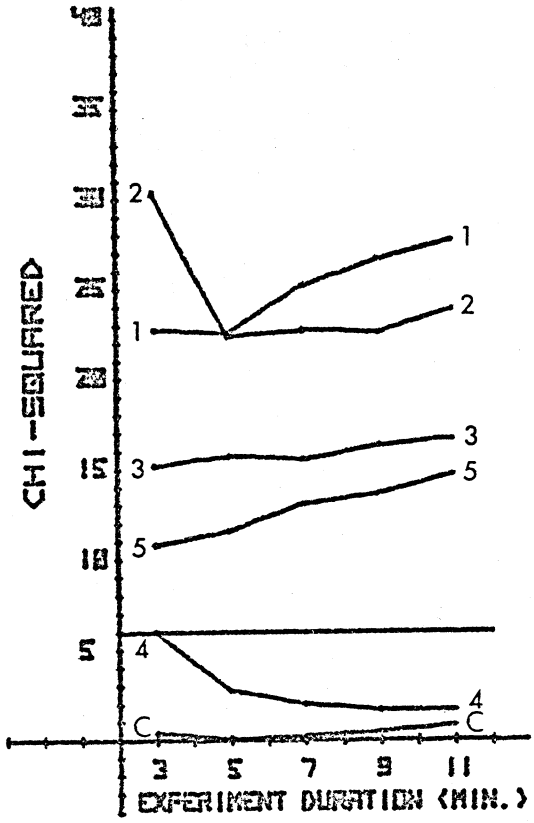
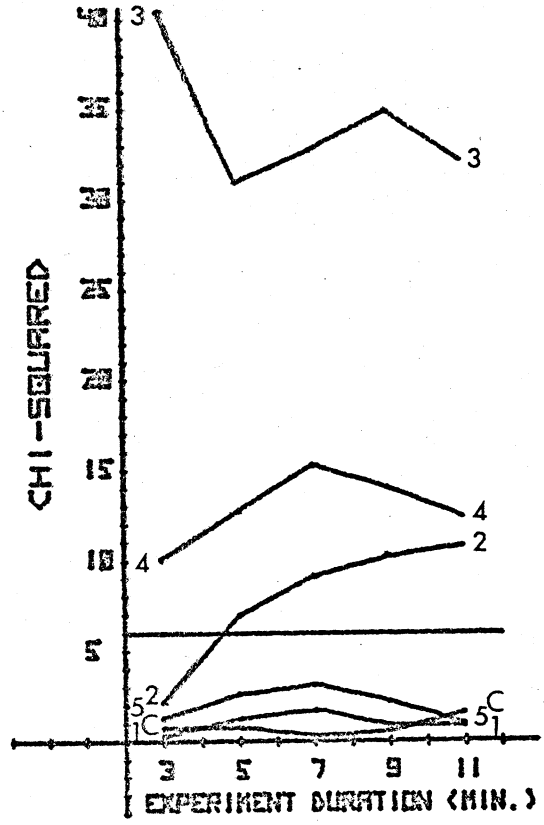


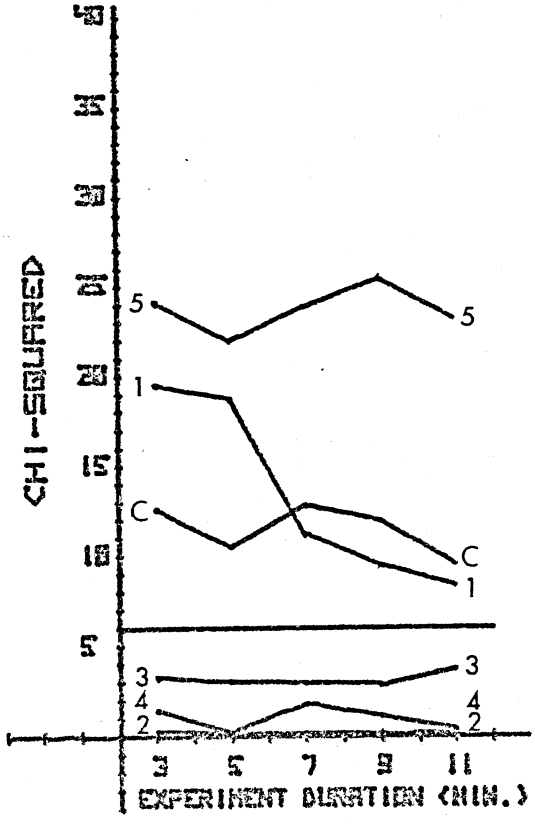
Figure 13. Chi-squared values for five different balanced intervals of each playback experiment. The horizontal line at 5.99 is the acceptance level for chi-squared with alpha equal to 0.05 and two degrees of freedom. Points falling above the line at 5.99 are significant. The horizontal axis is the interval tested - e.g. experiment duration of seven minutes indicates that three pre-playback minutes, three post-playback minutes and the minute of playback were used in computing chi-squared. Chi-squared values were not calculated when data was insufficient to apply the test. This proved to apply only to data collected for Number of Peep Vocalizations as seen in D. Symbols next to the plots indicate the playback vocalization (1 = Peep-Chuck, 2 = Trill, 3 = Whine, 4 = Chatter, 5 = Scream, C = Chickadee Control).



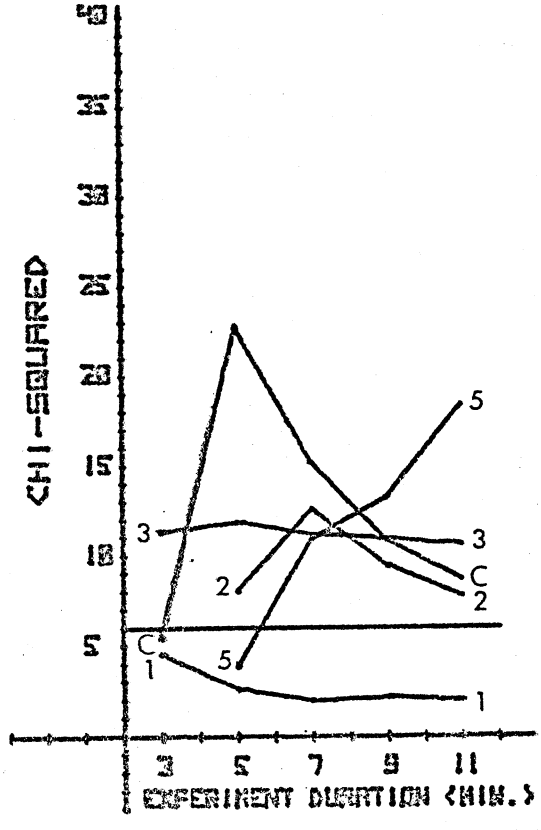
A. Seconds Alert



B. Seconds Oriented to Speaker



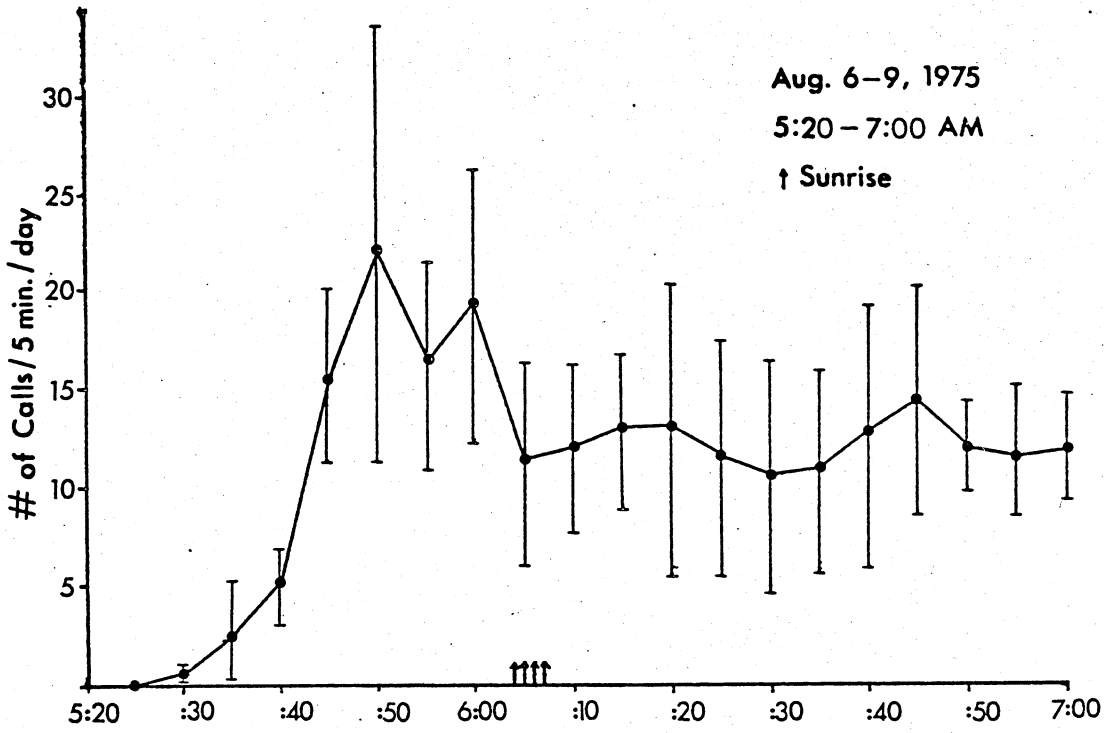
C. Seconds in Tree

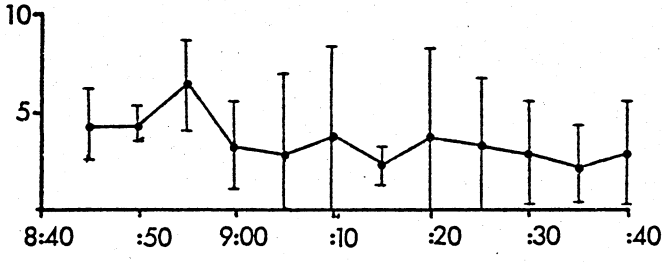


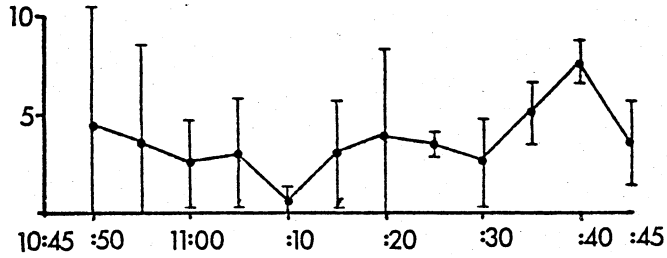
D. No. of Peep Vocalizations

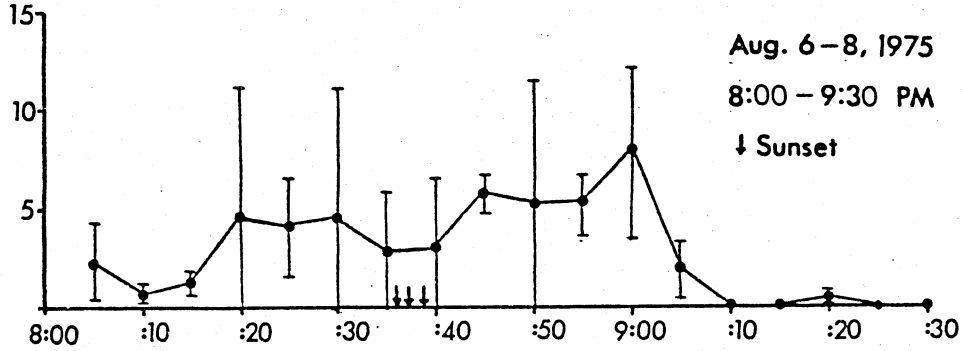
Figure 14. Daily Chatter activity in early August 1975. Each data point indicates the average number of Chatters heard per day during a five minute interval. Brackets indicate plus and minus one standard deviation. Sunrise was getting later with each day and sunset was getting earlier. All occurences of Chatters were recorded from one location within the study area.

CHATTER VOCALIZATIONS









APPENDIX B:

TABLES

Table 1. Sound pressure levels of red squirrel vocalizations measured directly with a sound level meter. Sound pressure level accuracy of meter used was ± 2 db. All SPL measures are in db units, RE: 0 db = 0.0002 dynes/cm^2.

Squirrel ID	Vocalization	Distance to mic.	Orientation to mic.	Lab or Field	SPL Range	Av. SPL
DM35♀						
	Peeps	2.9m	120°	Field		<60
	Trill	2.8-2.5m	135°	Field		64
DM148♀						
	Peeps	1.3-1.6m		Field		<60
	Trill	3.0-3.5m		Field		64.5
	Chucks & Peeps	6.0m		Field		<60
Unmarked						
	Chatter	3.0m	120°	Field		64
	Chuck	2.4m	180°	Field		<60
	Many Peeps & a Trill	6.9m	120°	Field		<60
DM15♀						
	26 Peeps	0.5m	0°	Lab	68-72	
	3 Chucks	0.5m	0°	Lab		>76
	32 Peeps	0.5m	0°	Lab	76-79	77.95
	24 Chucks	0.5m	0°	Lab	80-85	82.3
	4 Peeps	0.5m	45°	Lab	78	78
DM58♀ and DM14♂						
	14 Peeps	0.3-0.4m	0-90°	Lab	64-75	69.0
	3 Chucks	0.3-0.4m	0-90°	Lab	79-80+	79.3+
	4 Growls[1]	0.4m	0°	Lab		64
DM4♀						
	2 Growls[2]	0.3m	180°	Lab	64-68	
	Chuckles	0.2m	0°	Lab		<60

[1] Four, three to eight note Growl sequences of from 0.5 to 1.5 seconds duration.

[2] One 8.5 second 47 note Growl sequence and one 11.5 second 56 note Growl sequence.

Table 2. Decibel levels of red squirrel sounds at 1 meter. Sound pressure level accuracy of meter used was ± 2 db. All measures RE: 0 db = 0.0002 dynes/cm^2. Except where noted, sound levels not measured at 1 meter were standardized to that distance assuming inverse square attenuation. N = sample size. N' = subset of N that had to be standardized to 1m. Data combined for all squirrel orientations.

Type	Where Measured	# of Subjects	N(N')	Av. Peak db	db Range
Peep[1]	Field	1	3 (0)	68.0	67.0-69.0
Peep	Lab	3	242(239)	65.5	53.5-72.0
Chuck[2]	Field	1	1 (1)	80.0	80.0
Chuck	Lab	3	35 (35)	75.0	66.5-79.0
Growl[3]	Field	2	35 (0)[4]	68.6	60.0-73.0
Growl[3]	Lab	3	36 (36)	60.9	49.5-71.0
Chatter	Field	5	11 (4)	72.4	64.0-80.0
Whine[5]	Field	1	8 (0)	66.9	64.0-70.0
Trill	Field	3	3 (3)	78.0	74.0-85.0
Scream	Lab	1	4 (3)	65.9	61.5-74.0
Chuckle[6]	Lab	1	1 (1)	46.0	46.0
Drumming	Lab	1	2 (2)	59.0	59.0

[1] Peak db of three series of harmonic Peeps (17, 15, and 3 Peeps) made during an intense interaction. Measurement of other Peeps or Peep series made by five subjects in the field from 1.3 to 10m were all less than 60 db.

[2] Peak db of Chucks from two other subjects in the field at 2.4 and 6m were both less than 60 db.

[3] Each "Growl" here consists of three to 48 Growl notes in a series lasting from 0.5 to 9.0 seconds.

[4] No standardization to 1 meter. All Growls occurred between 0.7 and 1.6m from the microphone but exact distance for each vocalization is unknown.

[5] Series of Whine notes lasting from 1.0 to 4.0 seconds.

[6] Fifteen Chuckles given in the lab at 0.1 to 0.2m were all less than 60 db.

Table 3. Distribution of playback experiments and duration of vocalizations played back. Playbacks of the Trill were discontinued as of 8 April 1976 (see text). One playback of a Chatter to a female included in this table was voided due to outside human interference at the time of playback and is excluded from analysis. Playbacks were repeated three times for the Trill, Whine, Chatter, and Scream during the minute of the playback. The Chickadee control and Peep-Chuck sequence were continuous playbacks of sixty seconds duration.

		Played Back Vocalization						
		1 Peep-Chuck	2 Trill	3 Whine	4 Chatter	5 Scream	6 Chickadees	Row Total
Respondant	♂	5	1	3	3	3	2	17
	♀	3	1	4	2	4	3	16
	?	0	0	1	2	0	2	5
	—	—	—	—	—	—	—	—
Column Total		8	2	8	7	7	7	39
Duration (Seconds)		60	5	9	3.5	3.5	60	

Table 4. Sound Pressure Levels of playback recordings. SPL at 1 meter RE: 0 db = 0.0002 dynes/cm^2. All units are db. PB = Playback.

#	Vocalization	PB 1-6	PB 7-11		PB 12-39	Peak	Range
		lab	field	lab	field		
1	Peeps Chucks	62-66 69	64-67**	68-72**	66-71[1]	71	62-71
2	Trill	68**	67	69	79[2]	79	67-79
3	Whine	66-68**	63-66	66-68	72-76	76	63-76
4	Chatter	70	67	70	73	73	67-73
5	Scream	60-64	67-71	70-74	69-75	75	67-75
6	Chickadees	68-75	63-68**	68-72**	65-72	75	63-75

[1]Tape noise artifact peaks at 73 db at one point.
[2]The five Peeps preceding the Trill were at 70-71 db.
**No playbacks made of this vocalization in this set of experiments.

Table 5. Peep vocalizations. Acoustic behavior accompanying Peeps during observed cases of a few seconds to several minutes of Peep vocalizations from 17 December 1974 through 8 May 1976 involving 24 marked and several unmarked squirrels. A. Entries are: number of cases of occurrence (% of total # cases). B. Entries are: number of cases of occurrence (% of # cases of Peeps in that context).

A.

	In Trap	Upon Release	To Observer[1]	To Other Squirrel	Total
Peeps	14 (13.3)	14 (13.3)	51 (48.6)	26 (24.8)	105 cases

B. Accompanying acoustic behavior.

Chuck	2 (14.3)	2 (14.3)	16 (31.4)	14 (53.8)	34 (32.4)
Groan		4 (28.6)	6 (11.8)	8 (30.8)	18 (17.1)
Trill		2 (14.2)	16 (31.4)	3 (11.5)	21 (20.0)
Growl	2 (14.3)		1 (2.0)	9 (34.6)	12 (11.4)
Mult-Chuck				6 (23.1)	6 (5.7)
Chatter		3 (21.4)	5 (9.8)	3 (11.5)	11 (10.5)
Whine				3 (11.5)	3 (2.9)
Drumming		1 (7.1)	5 (9.8)	1 (3.8)	7 (6.7)

[1]Includes one case where a Trill followed by several Peeps was given as a squirrel escaped from a crow.

Table 6. Groan vocalizations. Acoustic behavior accompanying Groans during observed cases of one or more Groan vocalizations from 19 December 1974 through 8 May 1976 involving at least one unmarked and seven marked squirrels.

Groan 23 cases

Accompanying acoustic behavior	Cases of occurrence
Peep	22 (95.7%)
Chuck	14 (60.9%)
Trill	7 (30.4%)
Growl	6 (26.1%)
Multiple-Chuck	1 (4.3%)
Chatter	2 (8.7%)
Drumming	1 (4.3%)

Table 7. Chuck vocalizations. Acoustic behavior accompanying Chucks during observed cases of a single Chuck up to several minutes of Chuck vocalizations from 17 December 1974 through 9 April 1976 involving nineteen marked and several unmarked squirrels. A. Entries are: number of cases of occurrence (% of total # cases). B. Entries are: number of cases of occurrence (% of # cases of Chucks in that context).

A.	To Observer	To Conspecific	Total
Chuck	23 (42.6)	31 (57.4)	54 cases
B. Accompanying acoustic behavior			
Peep	19 (82.6)	17 (54.8)	36 (66.7)
Trill	8 (34.7)	1 (3.2)	9 (16.7)
Groan	5 (21.7)	6 (19.4)	11 (20.4)
Growl	1 (4.3)	10 (32.3)	11 (20.4)
Multiple-Chuck		6 (19.4)	6 (11.1)
Chatter	3 (13.0)	2 (6.5)	5 (9.3)
Whine		2 (6.5)	2 (3.7)
Buzz		1 (3.2)	1 (1.9)
Drumming	1 (4.3)		1 (1.9)

Table 8. Trill vocalizations. Acoustic behavior accompanying Trills during observed cases of one or more Trill vocalizations from 17 December 1974 through 7 May 1976 involving seventeen marked and several unmarked squirrels.

Trill	30 cases
Accompanying acoustic behavior	Cases of occurrence
Peep	22 (73.3%)
Chuck	9 (30.0%)
Groan	7 (23.3%)
Growl	4 (13.3%)
Chatter	3 (10.0%)
Drumming	1 (3.3%)

Table 9. Chatter vocalizations observed from 17 December 1974 through 21 May 1976 from 32 marked and several unmarked squirrels.
A. Sequence and occurrence of Whines accompanying Chatters.
B. Catagorical breakdown of how the Chatter was used.

A.	Pattern of Whine accompaniment to Chatters, 46 cases.		
	Chatter-Whines	34 (73.9%)	
	Whines-Chatter	9 (19.6%)	
	Whines-Chatter-Whines	2 (4.3%)	
	Chatter-Whines-Chatter	1 (2.2%)	
B.	Target of Chatter, 225 cases.		
	I. Chatter when no other squirrels near[1] (Includes release data and distant vocalizations where subject was unseen)	119 (52.9%)	
	- Answer calls[2]		25
	II. Chatter at observer	26 (11.6%)	
	III. Chatter at a specific squirrel	58 (25.8%)	
	- Chatter with Whines		20
	- Displacements		17[3]
	IV. Chatters given during mating chase	22 (9.8%)	
	- by males		19
	- by female		3

[1] Observer not believed to be the stimulus in these cases.
[2] "Answer calls" are Chatters that are believed to be given in direct response to another Chatter.
[3] Includes one case where a Tamius striatus was displaced. In the three cases where a Chatter with Whines did not displace a squirrel, the subject being vocalized at was in a trap and unable to move out of the area.

Table 10. Whine vocalizations observed from 19 December 1974 through 8 May 1976 from eighteen marked and several unmarked squirrels in 66 cases.

Whine occurs with Chatter	46 (69.7%)	
Whine occurs alone (without Chatter)	20 (30.3%)	
Vocal target displaced		9
Vocalizer gives Whines after being displaced		3

Table 11. Multiple-Chuck vocalizations. Acoustic behavior accompanying Multiple-Chucks during observed cases of Multiple-Chuck vocalizations from 19 December 1974 through 22 December 1975 involving at least one unmarked and five marked squirrels.

Multiple-Chuck	12 cases
Accompanying acoustic behavior	Cases of occurrence
Peep	4 (33.3%)
Chuck	5 (41.7%)
Groan	1 (8.3%)
Growl	3 (25.0%)

Table 12. Growl vocalizations. Acoustic behavior accompanying Growls during observed cases of one or more Growl vocalizations from 4 January 1975 through 9 April 1976 involving seventeen marked and at least one unmarked squirrels.

Growl	52 cases
Accompanying acoustic behavior	Cases of occurrence
Peep	12 (23.1%)
Chuck	11 (21.2%)
Trill	4 (7.7%)
Groan	7 (13.5%)
Multiple-Chuck	4 (7.7%)
Chatter	3 (5.8%)
Whine	5 (9.6%)
Chuckle	2 (3.8%)
Drumming	1 (1.9%)

Table 13. Buzz vocalizations. Acoustic behavior accompanying Buzzes during observed cases of one or more Buzz vocalizations from 29 February 1976 through 9 April 1976 involving at least two unmarked and eight marked squirrels.

Buzz	22 cases
Accompanying acoustic behavior	Cases of occurrence
Chatter	9 (40.9%)
Whine	1 (4.5%)
Chuck	1 (4.5%)
Drumming	1 (4.5%)
Tail wagged in leaves	1 (4.5%)

Table 14. Acoustic behavior upon release from live trap at the site of capture after having been captive for a few minutes up to over an hour. Observations of the squirrels up to five minutes after being released were considered in tabulation of vocalizations made after release. Data presented in A are from releases where all vocalizations were noted upon release. Only the presence or absence of Chatter vocalizations was noted for the data presented in B.

A. 42 releases (22 individuals) from 12-21-74 through 12-29-75.	
No vocalizations	15 (35.7%)
One or more Chatters	13 (31.0%)
Peeps followed by one or more Chatters	3 (7.1%)
Peeps or Peeps accompanied by Groans, Chucks, or Trills	10 (23.8%)
Type of vocalization not noted	1 (2.4%)
B. 68 releases (36 individuals) from 12-21-74 through 1-1-76.	
No Chatters	44 (64.7%)
One or more Chatters	24 (35.3%)

Table 15. Behavioral function of red squirrel vocalizations.

Vocalization		Major Function
Peep	Alert ↓ Alarm	Visual contact "Alarm" calls
Groan		
Chuck		
Trill		
Scream		Physical contact "Alarm" call (Distress)
Chatter		Territorial Announcement
Whine	Distant warning	Aggressive Intent
Multiple-Chuck	Closer proximity warning	
Growl	Intense immediate encounter	
Chuckle	Mild immediate encounter	
Buzz		Appeasement